ON THE STRUCTURE, DISTRIBUTION AND FUNCTION OF THE NERVES WHICH INNERVATE THE VISCERAL AND VASCULAR SYSTEMS. By W. H. GASKELL, M.D., F.R.S. (Plates I. to IV.)

PART I. THE EFFERENT NERVES OF THE VASCULAR AND VISCERAL MUSCLES.

Chapter I. The structure and distribution of these nerves.

THE efferent nerves of the body can be divided into groups according to their function. Thus we speak of the motor and inhibitory nerves of muscular structures, of the trophic and secretory nerves of glandular structures, of the trophic nerves of the skin &c. Such terms represent either purely artificial and hypothetical divisions of the efferent nerves, or else they possess a deeper signification and describe real fundamental divisions of the nervous system. In the latter case the physiological differences must be bound up with morphological differences so that a group of nerves of the same function must be capable of being grouped together under the same morphological laws of structure and distribution. The simplest example of such correlation between structure, distribution and function is to be found in the motor nerves of ordinary skeletal muscles. We know that they pass from the spinal cord in the anterior roots of the spinal nerves, that they consist of large medullated nerve fibres, and that their function remains the same in all parts of their course. Such nerves possess a real and not a hypothetical existence because the anatomical, histological and physiological proofs of such existence are all in harmony, and point to one and the same nerve structure as the motor nerve of the skeletal muscle.

If the various nerves of different function which are described as innervating the viscera have a similar real and separate existence, then

in their case also a similar correlation must exist between their function and their morphological arrangement.

I propose in a series of papers to deal with this question for all the different groups of nerves, classifying them according to function, and including afferent as well as efferent nerves. In this present paper I shall confine myself to the efferent nerves.

These may be divided into three groups as follows :

1. Nerves of the vascular muscles.

   (a) Vaso-motor, i.e. vaso-constrictor, accelerators and augmentors of heart.

   (b) Vaso-inhibitory, i.e. vaso-dilators and inhibitors of heart.

2. Nerves of the visceral muscles.

   (a) Viscero-motor.

   (b) Viscero-inhibitory.

3. Glandular nerves.

I propose at present to deal chiefly with the efferent nerves of the vascular and visceral muscles, leaving the glandular nerves to be considered more fully in a subsequent paper.

In any attempt to trace out the relation existing between the structure, distribution and function of these nerves it is advisable in the first instance to confine oneself to the same animal. I have therefore limited myself to the dog, choosing this animal as my type partly because of the close resemblances between the distribution of its nerves and that of the nerves of man, and partly because our knowledge of the functions of the majority of the visceral nerves is based upon experiments conducted upon this animal.

The distribution of the visceral nerves in the dog, in their course from the central nervous system to the periphery, is most conveniently and systematically described by their division into three regions, viz. (1) those which arise from the thoracic portion of the spinal cord, (2) those which arise above that region, and (3) those which arise below it.

SECTION 1. *The nerves of the thoracic region.*

In the thoracic region we find the typical spinal nerve of the morphologist with its division into three branches, dorsal, ventral and visceral. The visceral branch or *ramus communicans* passes from the spinal nerve into the main sympathetic chain, i.e. into a chain of ganglia which lie close against the bodies of the vertebræ and may be called the chain of vertebral or lateral ganglia. From this chain

nerves pass into a second line of ganglia, viz. the semilunar, inf. mesenteric &c., which are prevertebral in position, are connected together into a more or less distinct chain, and may be called the chain of prevertebral or collateral ganglia; the nerves which pass from the lateral to the collateral chains may be called after Milne Edwards[1] the *rami efferentes*. From this chain again nerves pass to the organs themselves and, in the tissue of or in the immediate neighbourhood of the organs, are again in connection with ganglion cells which may be described as the terminal ganglia.

In addition to these various sets of ganglia, we have the ganglia of the posterior roots or root ganglia, with which it is possible for the visceral nerves to have connection. We have therefore four sets of ganglia in possible connection with each *ramus visceralis*, two of which, viz. the root ganglia and the lateral ganglia, may be spoken of as proximal, and two, the collateral and terminal ganglia, as distal.

Further, although the *ramus visceralis* of the morphologist is definite in its meaning, the same cannot be said of the *ramus communicans* of the physiologist. By the latter term physiologists and anatomists include as pointed out by Onodi[2] two distinct structures, the one composed mainly of medullated, and the other of non-medullated nerve-fibres. We can in fact in the thoracic region speak of each *ramus communicans* as composed of two parts, a white and grey ramus.

The distribution of the white ramus. The medullated fibres of the white *ramus communicans* can be traced in the one direction into both the anterior and posterior roots of the corresponding spinal nerve ; in the other direction partly into the main sympathetic chain or chain of lateral ganglia, partly as pointed out by Onodi into the nerves forming the splanchnics, and so to the chain of collateral ganglia, without entering into connection with the ganglia of the lateral chain.

Further, these white rami communicantes are only found in connection with a limited region of the spinal cord. On Plate III. Fig. 1, I give a figure representing somewhat diagrammatically the arrangement of the visceral nerves in the dog ; the *rami communicantes* are coloured red and blue respectively according as they are composed mainly of medullated or non-medullated nerve fibres.

The first white ramus is found in connection with the 10th spinal nerve, i.e. the second thoracic nerve, the last in connection with the 25th spinal or 2nd lumbar nerve. Above and below these two

[1] *Leçons sur la physiologie*, Tome XI. p. 337.
[2] *Archiv f. Anat. u Physiol. Anat. Abtheil.* 1894, p. 145.

limits the rami communicantes belong exclusively to the grey group. Thus the *radix brevis* and *longa* or *vertebralis* from the first thoracic ganglion or ganglion stellatum, the so-called rami communicantes of the inferior and superior cervical ganglia, the rami communicantes of the lower lumbar and sacral nerves all show the same structure as the grey rami, and belong therefore to that group and not to the group of white rami[1].

Further, the arrangement of the white rami is peculiar; the white rami of the 10th, 11th, 12th, 13th nerves (2nd, 3rd, 4th, 5th thoracic) are, as noticed by D a s t r e and M o r a t[2] and O n o d i[3], directed upwards, those below the 5th thoracic are directed mainly downwards. The reason for this difference of direction is evident. Most of the upward directed fibres can be traced over the ganglion stellatum along the two branches of the annulus of Vieussens past the inferior cervical ganglion along the cervical sympathetic up to the superior cervical ganglion; while those which are directed downwards pass off largely from the lateral chain of ganglia to form the splanchnic nerves. Further, as we pass down the lateral chain of ganglia into the sacral region we find again, as O n o d i[4] has noticed, that the medullated fibres in that chain become fewer and fewer, so that in the sacral ganglia themselves we have at last only non-medullated fibres present.

In fact the white rami communicantes are formed by an outflow of medullated nerves from both anterior and posterior roots of the spinal nerves between the second thoracic and second lumbar inclusive, which medullated nerves pass not only into their metameric sympathetic (lateral) ganglia, but also form three main streams, upwards into the cervical ganglia, downwards into the lumbar and sacral ganglia, and outwards into the collateral ganglia.

The distribution of the grey ramus. If we turn our attention now to the grey rami communicantes we find that in their distribution as well as in their structure they differ markedly from the white rami. In the first place each grey ramus is intimately connected with its corresponding lateral ganglion, its fibres are directly in connection with the nerve cells of that ganglion, none of its nerve fibres pass over the

---

[1] N.B. In the preliminary communication to this paper (*Proceedings of Physiological Society*, Feb. 14, 1885) I said that the first white ramus belonged to the 1st thoracic nerve. Subsequent dissection and more careful counting has shown that in all cases the nerve in question is the 10th spinal nerve; i.e. the 2nd not the 1st thoracic.

[2] *Système nerveux vaso-moteur*, Paris, 1884.

[3] *Op. cit.*   [4] *Op. cit.* p. 163.

ganglion to proceed to more distant parts as in the case of the white rami; further, as we trace this grey ramus towards its corresponding spinal nerve we find that it usually sends off branches which ramify in the connective tissue overlying the vertebræ. It is on these branches that the accessory ganglia noticed in anatomical works have been found. Such branches may be so numerous, that ultimately, when the spinal nerve is reached, the originally thick grey ramus is reduced to the finest thread of fibres, which becomes lost on the sheath or among the fibres of the spinal nerve itself. In other cases, and this is especially evident with the grey rami of the brachial and sciatic plexuses, the non-medullated fibres can be followed easily into the spinal nerve itself, where they can be seen to divide into two directions, the one set passing peripherally, the other centrally. Of the non-medullated nerves which pass centralwards, most of them pass into the sheath of the nerve and are lost in the dense layers of connective tissue found in connection with the inter-vertebral foramen. Some few may still pass centralwards into the spinal nerve itself, and so be connected with the central nervous system. As it was impossible to trace them directly, I determined to decide this question by the examination of the structure of the anterior and posterior roots after careful staining with osmic acid. The roots of each spinal nerve can be divided into two separate portions, the part between the dura mater and the cord, and the part between the dura mater and the root ganglion. The former portion is formed by a series of separate rootlets which upon penetrating the dura mater receive a connective tissue investment, and combine together to form the distinctive anterior or posterior root.

No great distinction exists between the structure of the anterior root outside the dura mater and any one of its rootlets within the dura mater; a slightly greater amount of connective tissue is found investing and penetrating between the medullated nerve fibres of the former than of the latter; in neither is there the slightest trace of any non-medullated fibres to be found. In the posterior roots (outside the dura mater), on the other hand (as pointed out by Reissner)[1], a considerable amount of connective tissue can be seen in between the medullated fibres, and appearances indicative of non-medullated nerve fibres are apparent in this connective tissue matrix when sections of the roots are examined. If however the posterior rootlets (inside the dura mater) be examined,

[1] Reichert's *Archiv*, 1862, p. 125.

then it is seen that the connective tissue matrix has disappeared almost entirely, and with it have passed away all traces of non-medullated fibres; the medullated fibres of the posterior rootlets between the dura mater and the cord stand out nearly as clear from admixture with foreign elements as those of the anterior rootlets. Again, by means of a series of sections cut through the posterior roots with the dura mater left in situ, it is easy to see how the connective tissue matrix with its included non-medullated fibres separates out from among the medullated nerves of the roots and passes away into the dura mater itself. Similarly, doubtless the small remnant found in the posterior rootlets themselves passes off into the pia mater and arachnoid membranes.

I can therefore assert confidently that no non-medullated nerves leave the central nervous system either in the posterior or in the anterior roots, any such nerves being in reality peripheral nerves for the supply of the spinal membranes.

Putting together all the facts mentioned, the conclusion is evident that the grey rami communicantes spring from the ganglia of the lateral chain and pass peripherally to supply the corresponding spinal nerves together with the vertebræ[1] and spinal membranes. They are in fact peripheral nerves of the same kind as many others which arise from the chain of lateral ganglia.

So far we arrive at this important conclusion.

The white rami communicantes alone constitute the rami viscerales of the morphologist. The outflow of visceral nerves from the central nervous system into the so-called sympathetic system takes place by their means alone, and is therefore limited in the thoracic region to that part of the spinal cord which is included between the origins of the 10th and 25th (2nd thoracic and 2nd lumbar) nerves inclusive.

Further, in strict accordance with the limits of these thoracic white rami we find a marked change of structure in the roots of the spinal nerves. This change is most pronounced in the anterior roots, and in my description I shall therefore confine myself to them. In the anterior roots of the cervical nerves we find upon section of osmic preparations nerve fibres of varying sizes, see Pl. I. Fig. 3, most of which are of large calibre, varying from $14 \cdot 4\ \mu$ to $19\ \mu$ or larger. Scattered in among these we find others of smaller size and here and there, not

---

[1] Luschke quoted in Henle, *Anatom. d. Mensch.*

grouped together but isolated among the others, a few fine fibres which are never less than 3·6 μ, the commonest size for these, the smallest fibres to be found in these roots, being from 4·5 μ to 5·4 μ. Such a description holds good for the anterior roots of the first 9 spinal nerves; the anterior root of the 10th nerve (2nd thoracic) is however markedly different; suddenly in this root large numbers of medullated nerves make their appearance of a finer calibre than the smallest of those in the preceding groups; fibres of sizes varying from 1·8 μ to 2·7 μ occur in large quantities arranged together in groups which include a few as large as 3·6 μ. These bundles of the very finest fibres lie in among fibres of the same size as those which occur in the preceding roots; here too fibres corresponding in size to those of the smallest which are found in those roots are still present in the same isolated manner as before. In fact the anterior root of the 10th nerve differs from that of the 9th nerve (see Figs. 7, 6, Pl. II.) neither in the size nor arrangement of its largest nerve fibres but in the one fact that it contains something new, something which is wanting in the anterior roots of the preceding nerves, viz. bundles of finest medullated nerve fibres[1].

An examination of the anterior roots below the 10th (2nd thoracic) shows that the same bundles of exceedingly fine medullated nerves are present in these roots until we arrive at the 26th (3rd lumbar) nerve. Here again we find a return to the structure of the cervical anterior roots; the bundles of the finest fibres have entirely disappeared.

A comparison of these roots between the 10th and 25th nerves brings out the further fact, that whereas these bundles come in at the 10th root with great suddenness and in large numbers they thin down in numbers more gradually as they approach the lower limit; root 23 (last thoracic) contains them in large quantities; in roots 24 (1st lumbar) they are certainly fewer in number, and in root 25th they are fewest of all. In accordance with this variation in the amount of these nerves in the anterior roots we find that the *white ramus communicans* of the 10th nerve is one of the largest of all, while those of the 24th and 25th are the thinnest and most inconspicuous. Finally, the part which these bundles of very fine medullated nerves play in the formation of the ramus visceralis is proved absolutely by the facts that they can be traced into the white ramus communicans, and that the structure of the latter is almost entirely composed of such fibres.

---

[1] Reissner (*Op. cit.*) notices this peculiarity of the anterior roots in the thoracic region, without however giving any explanation of it.

In Pl. II. Figs. 8, 9, I give a drawing of the white ramus communicans of the 11th nerve (3rd thoracic) together with a drawing of the ramus communicans (typical grey) of the 26th nerve (3rd lumbar).

In the first we see that almost all the fibres are medullated of the very finest size with a few larger medullated fibres and a small amount of non-medullated. In the 2nd almost all the fibres are non-medullated; a few large medullated are scattered here and there, no groups of fine medullated are to be found.

Further, we can trace these same fine medullated fibres along the lines of outflow of the thoracic visceral nerves.

Upwards the same bundles of medullated nerve fibres of the same extreme fineness of calibre constitute the main portion of the annulus of Vieussens; they can be traced as a fine white nerve within the sheath of the conjoint vago-sympathetic into the superior cervical ganglion; here they are lost and can be traced no further. The other nerves with which this ganglion is in connection are without exception mainly composed of non-medullated fibres with stray medullated ones among them.

Downwards they form the main sympathetic or lateral chain, thinning off in number as we examine the lower portion of the chain until in the sacral ganglia and their connections they finally disappear.

Outwards they pass over the lateral ganglia to form the main portion of the splanchnic nerves and the other rami efferentes and thus pass into the collateral ganglia, beyond which again they cannot be traced.

So far then I have demonstrated that an outflow of visceral nerves takes place from the central nervous system between the 2nd thoracic and 2nd lumbar nerves, which visceral nerves can be recognized not merely by the presence of white rami communicantes but also by the smallness in calibre of the visceral nerve fibres.

We come now to the examination of the distribution of the visceral nerves above and below this region, and first, because it is simplest, I will take the region below, that is the lumbo-sacral region.

SECTION II. *The nerves of the lumbo-sacral region.*

As already mentioned the anterior roots of the 26th nerves (3rd lumbar) resemble in their structure those of the cervical nerves; so too do those of the 27th, 28th and 29th (4th, 5th lumbar and 1st sacral) nerves.

When however we reach the 30th and 31st (2nd and 3rd sacral) roots we find again an inflow of nerve fibres of the smallest calibre; tracing these outwards we find that they leave the 2nd and 3rd sacral nerves to constitute the main portion of the *nervi erigentes*. These nerves, as is well known, pass directly to the hypogastric plexus without communicating with the lateral chain of ganglia; from the hypogastric plexus they send branches in two directions, upwards to the inferior mesenteric ganglion, downwards to the bladder, rectum and generative organs. They resemble therefore, in their structure, in their method of formation and in their passage directly to the collateral ganglia without entering into the lateral ganglia, the medullated nerve portion of the splanchnic nerves; they constitute the *rami viscerales* of the sacral region, and differ from the corresponding rami viscerales of the thoracic region simply in the fact that they pass directly into the ganglia of the collateral chain alone, whereas the latter communicate directly with the ganglia of both the lateral and collateral chains.

Seeing then the importance of these nerves in any consideration of the visceral nervous system, their resemblance to the splanchnics and the differences of function of the fibres of which they are composed, it will be better to designate them by some more general title than *nervi erigentes*. I propose therefore to call them the *pelvic splanchnic* nerves. In accordance with this term I would call the rami efferentes which pass downwards to the semilunar and inferior mesenteric ganglia in connection with the thoracic outflow of visceral nerves the *abdominal splanchnic* nerves, and those which pass upwards to the superior cervical ganglion and constitute the cervical sympathetic, the *cervical splanchnic* nerves.

In the sacral region then we find another outflow of visceral nerves which similarly to those of the thoracic region can be traced to their respective ganglia, i. e. the ganglia of the hypogastric plexus and the inferior mesenteric ganglia, and can be recognized by the characteristic size of their medullated nerve fibres. (Cf. Pl. III. Fig. 1.)

SECTION III. *Nerves of the cervico-cranial region.*

If we now turn our attention to the region above the thorax we find, as already mentioned, that the anterior roots of the upper spinal nerves do not contain any bundles of medullated fibres of the smallest calibre, and in accordance with this fact they do not give rise to any white ramus communicans. In other words, with the absence of the characteristic nerve fibres in the roots we find a coincident absence of

rami viscerales. Before however we can conclude that the cervical nerves are devoid of rami viscerales and that therefore they divide only into two branches, dorsal and ventral, we must be sure that our examination includes the whole of each cervical nerve. Now, as is well known, each of the upper cervical metameres gives origin not only to the anterior and posterior roots of the corresponding cervical nerve but also to the roots of the spinal accessory; roots which from their origin and position we may provisionally call *lateral*. We must therefore in our search for the cervical rami viscerales examine not only the anterior and posterior but also the lateral roots of these nerves.

In Pl. IV. Fig. 7, I give a picture of a section of the spinal accessory just before it reaches the ganglion jugulare of the vagus. The roots of the medullary portion of the accessory and of the vagus were carefully hardened in situ with osmic acid, the whole with a portion of the medulla oblongata removed, imbedded in paraffin, and "ribbons" of consecutive sections made through the whole of the nerve roots from the medulla oblongata up to and beyond the ganglion trunci vagi. The whole series of sections was mounted in order, every nerve fibre was well stained and remained on the slide in the exact position it occupied when imbedded. In Pl. II. Fig. 10, the arrangement of the fibres when imbedded is reproduced.

The figure shows that the spinal accessory is divided into two distinct portions, the one (*A*) composed of large medullated fibres with a few isolated medium sized ones among them, the whole of that portion being remarkably free from connective tissue; the other portion (*V*) composed mainly of the smallest medullated fibres among which are a few large ones imbedded in a conspicuous matrix of connective tissue. As we pass downwards in our examination of the roots of the spinal accessory we find that the portion which contains these very fine medullated fibres is formed by the upper roots of the nerve, i. e. by roots which arise with the vagus, and with the 1st, 2nd and probably 3rd cervical nerves. As yet I have not traced the lower limit of origin of these fine fibres. In Pl. I. Figs. 1, 2, I give an accurate representation of one of the medullary roots and of the large fibred portion of the nerve.

In this portion of the spinal accessory then we again meet with bundles of the same fine medullated nerve fibres which we have found to characterize the ramus visceralis in the thoracic and sacral regions.

Further, if we follow the series of sections in the outward direction, i. e. towards the ganglion trunci vagi, we find that the whole accessory

nerve passes by the ganglion jugulare vagi and then divides into two branches, the external and internal branch. The external branch which supplies the sterno-cleido-mastoid and trapezius muscles and joins the cervical plexus carries off the whole of the large-fibre portion (*A*) of the nerve. The internal branch (*V*) with its bundles of visceral small fibres passes into the vagus and can be traced directly into the *ganglion trunci vagi.*

We see then that in its formation and in its connection with the ganglion trunci vagi we can look upon the internal branch of the spinal accessory as formed by the rami viscerales of the upper cervical and vagus nerves.

Further, in the roots of the vagus itself and of the glossopharyngeal, we find again these bundles of small fibres in connection with the ganglion trunci vagi and ganglion petrosum respectively.

So too they are present in the chorda tympani, small petrosal and other cranial visceral nerves.

We can therefore speak of an outburst of visceral nerves in the upper cervical and cranial region of the same character as those in the thoracic and sacral regions. (Cf. Pl. III. Fig. 1.)

As I am desirous in this part of my paper to follow out the further course of these fine medullated nerves in connection with their function, I do not think it advisable to discuss here the homologies between spinal and cranial nerves, and will therefore leave the morphology of the cranial nerves to be dealt with subsequently. In an appendix to this paper I propose to treat more fully of the nature of the vagus and glossopharyngeal nerves.

We can sum up the distribution of visceral nerves so far as follows :

They issue from the central nervous system in definite sacral, thoracic and cervico-cranial regions.

From these regions they pass out into the ganglia of the visceral system.

From the sacral region they pass out in a single stream to the ganglia of the collateral chain.

From the thoracic region they pass out in a double stream, one to the ganglia of the lateral chain, the other to the ganglia of the collateral chain.

From the upper cervical region they pass out in a single stream to the ganglia on the main stems of the vagus and glossopharyngeal nerves.

The next step is to trace these nerves to their destination beyond

these ganglia. As however it is hopeless at present to follow any nerve or group of nerve-fibres through a mass of ganglion cells with which it is in connection, it is impossible by simple anatomical investigation to trace these nerves further; the course of a nerve-fibre can however be traced by its physiological action as well as by its histological characters; the further search must combine together the facts obtained from physiological experimentation with the records of anatomy and histology.

Seeing then that we must of necessity turn now from the consideration of the visceral nerves as a whole to the distribution of nerves of particular function, I have thought it best to arrange the further sections of this paper in accordance with special function rather than with special anatomical regions. Such an arrangement leads naturally to two great groupings into motor and inhibitory nerves respectively; I shall therefore commence with the vaso-motor nerves, including in this term, as already mentioned, the vaso-constrictor nerves and those which augment and accelerate the action of the heart.

SECTION IV. *On the structure and distribution of the vaso-motor (vaso-constrictor, and augmentor, accelerator) nerves.* (Pl. III. Fig. 2.)

We know with absolute certainty that the origin of all vasomotor nerves is to be found in the central nervous system; stimulation of the spinal cord is able to cause both augmentation and acceleration of the heart's action, and constriction of blood-vessels in all parts of the body; we know further that such nerves leave the spinal cord in anterior roots, from which they pass to the sympathetic system and are thence distributed to the heart and blood-vessels of the body.

Again, if we confine our attention for the moment to the cardiac (accelerator, augmentor) nerves of this group, we find from the experiments of Stricker and Wagner[1] that they are to be found in the main sympathetic (lateral) chain below the ganglion stellatum, and that they increase in number as the ganglion stellatum is approached. Seeing then that they leave the cord in anterior roots (in the frog in the anterior root of the 3rd nerve), that they pass from below upwards into the ganglion stellatum, it follows (because the anterior roots contain only medullated fibres) that they pass out from the central nervous system in the white rami (or rami viscerales) of the 2nd, 3rd and lower thoracic nerves, and that therefore in their passage to the ganglia of the lateral chain they are recognisable as forming part of those bundles of very fine

[1] *Sitzb. der k. Akad. der Wissensch.* 1878.

medullated nerve-fibres which we have already found to form the ramus visceralis and to be characteristic of the anterior roots in this region.

From the ganglion stellatum they either pass directly to the heart or else reach that organ from the annulus of Vieussens and the inf. cervical ganglion.

When examined in their passage from these ganglia they are found to be without exception non-medullated. I know no other bundle of nerve-fibres possessing a definite function which are so completely free from medullated fibres, large or small, as these cardiac nerves. Preparations obtained from the rabbit are specially instructive since in this animal the depressor nerve can be easily traced. When the so-called accelerators are examined near the heart both medullated and non-medullated fibres are found in them; upon tracing these further along towards the inf. cerv. ganglion it is easily seen that all the medullated fibres pass off into the depressor while non-medullated alone rise from the inf. cerv. ganglion.

Further, as I have previously shown[1], the course of these nerves is exceedingly constant; in all animals which I have observed they arise from that ganglion which I in conjunction with H. Gadow[2] have called the *ganglion cardiacum basale.* This corresponds in the mammal to the *ganglion stellatum.*

It follows therefore conclusively that nerve fibres possessing the same function pass into this ganglion in the form of fine medullated fibres and pass out of it as non-medullated fibres. One conclusion only is possible, viz. that these fibres are the same, and that they have lost their medulla in the ganglion.

What is true of the cardiac accelerator nerves is true also of the vaso-constrictor nerves; everywhere we find the same evidence that they pass into the lateral chain of ganglia by way of the rami viscerales, and are therefore in this part of their course fine white medullated nerves; and pass from that chain to the various parts of the body as non-medullated nerves in the grey rami communicantes, or in other peripheral nerves.

Thus Cyon[3] has shown that the vaso-constrictor nerves for the anterior extremity pass out of the cord below the origin of the roots of the brachial nerves in the anterior roots of the 2nd and subsequent thoracic nerves and reach the brachial plexus by way of the ganglion

---

[1] This Journ. Vol. v. p. 46.

[2] This Journ. Vol. v. p. 362.

[3] Ludwig's *Arbeiten*, 1868.

stellatum. In their passage therefore to the lateral chain of ganglia, they must be included among the bundles of the finest medullated fibres already mentioned in the anterior roots and white rami of this region; while from the ganglion stellatum, the only path by which they can reach the nerves of the brachial plexus is through the grey rami of the *radix brevis* and *radix longa*; therefore in this part of their course they must have become converted into non-medullated fibres.

Similarly Heidenhain and Ostroumoff[1] have shown that the vaso-constrictor nerves for the foot leave the spinal cord to reach the sympathetic high up above the origin of the roots of the sciatic, and reach the sciatic nerves by way of the abdominal sympathetic chain. These nerves therefore must pass into the sciatic plexus by way of the grey rami communicantes of the nerves forming that plexus, and must therefore leave the lateral chain of ganglia as non-medullated fibres, while they pass out of the central nervous system in the anterior roots of the lower dorsal and upper lumbar nerves and therefore pass into the lateral chain among the fine medullated nerves of the white rami communicantes.

These three instances alone are sufficient to prove that the vaso-motor nerves lose their medulla in the ganglia of the lateral chain; further evidence is given by the mere presence of grey rami such as the ramus vertebralis which accompanies the vertebral artery, and those already described which branch to supply the vertebræ and membranes of the cord accompanying the blood vessels of those parts.

Again, the known paths for the vaso-constrictor nerves of the head and neck, and for the abdominal organs, point strongly to the conclusion that the laws of their distribution are the same as in all other cases.

The cervical sympathetic nerves, or cervical splanchnics, on the one hand, and the abdominal splanchnics on the other are we know from the experience of physiology the main channels of the vaso-constrictor nerves of the two regions respectively. The blood vessels of the face, of the ear, of the eye, of the salivary glands, of the tongue, even of the membranes of the brain all receive their vaso-constrictor nerves by the path of the cervical sympathetic (cervical splanchnics). The blood vessels of every organ in the abdomen receive their motor nerves from the abdominal splanchnics, i.e. from the splanchnic nerves or from the corresponding rami efferentes of the upper lumbar ganglia.

The vaso-motor nerves therefore for the head and neck as well as for the abdomen leave the spinal cord as fine medullated nerves in the

[1] Pflüger's *Archiv*, Bd. xii. s. 219.

rami viscerales of the thoracic region, and in all probability pass from the chain of lateral ganglia as the non-medullated fibres which are found both in the abdominal and cervical splanchnic nerves.

These nerves are doubtless connected also with the collateral abdominal ganglia and with the sup. cervical ganglion respectively; the difference between the effects of mere section of the cervical sympathetic and of ablation of the sup. cervical ganglion points distinctly to such a conclusion. Such a connection with two sets of ganglia need cause no surprise, for accessory ganglia are present in the course of the non-medullated cardiac nerves and in the branches of the grey rami communicantes, so that it is a common occurrence for ganglion cells to be formed in connection with purely non-medullated fibres. Also the lowermost ganglia of the lateral chain itself are according to Onodi in connection only with non-medullated fibres.

It is therefore highly probable that the non-medullated vaso-motor nerves after they have lost their medulla in the lateral ganglia are in connection with other ganglion cells before they reach their destination in the muscles of the vascular system.

So far we can sum up the results obtained as follows:

Vaso-motor nerves for all parts of the body can be traced as bundles of the finest medullated fibres (varying in size from $1.8\,\mu$ to $3.6\,\mu$) in the anterior roots of all the spinal nerves between the 10th and 25th (2nd thoracic and 2nd lumbar) inclusive, along the corresponding ramus visceralis to the ganglia of the lateral chain (main sympathetic chain) where they become non-medullated, and are thence distributed to their destination either directly or after communication with other ganglia.

The above statement holds good for all those cases where undoubted vaso-motor action has been discovered by physiological experiment, and so striking is the consensus between the anatomical paths, the histological features and the physiological action of these nerves, that I am inclined boldly to assert that in mammals *all* the vaso-motor nerves of the body of necessity leave the central nervous system in the outflowing stream of visceral fibres which occurs between the 2nd thoracic and 2nd lumbar nerves; that they all pass in that branch of the stream which is in connection with the lateral ganglia and lose their medulla in these ganglia. This chain might therefore most appropriately be called the chain of vaso-motor ganglia, instead of its present meaningless title of main sympathetic chain.

As however vaso-motor nerves have been asserted to leave the central nervous system by other paths, it is necessary to examine the evidence in their favour and see whether or no such nerves are absolutely confined within the limits assigned by me. In other words, is there any incontrovertible evidence that they pass out of the central nervous system in the roots of the cranial, sacral or cervical nerves?

Of all the cranial nerves two only have been accredited with the possession of vaso-motor fibres—the trigeminal and vagus—and of these two the evidence for the presence of such nerves in the former is based purely upon the vascular changes which occur in the eye in connection with the degenerative phenomena observed in the cornea after section of the trigeminal; the changes in question are of interest in connection with the question of trophic nerves and the effect upon the cornea of the removal of the sensory fibres for the eye, but clearly are insufficient to establish the existence of *motor* vascular nerves in the roots of the trigeminal. We are then reduced to the vagus in our search for cranial vaso-motor nerves.

This nerve has been supposed to contain such fibres for the heart, lungs, stomach and spleen; yet it can be safely asserted that in no single case is the evidence as clear and unmistakeable as in the case of all true vaso-motor nerves.

The supposed vaso-motor influence of the vagus upon the lungs is like that of the trigeminus upon the eye based simply upon hyperæmia of the lungs following section of the vagi, an hyperæmia which must be dissociated clearly from the degenerative changes following the section before we can discuss it as giving evidence of motor action. Again, hyperæmia of the stomach has been observed in consequence of section of the vagi, but in order to prove that hyperæmia is due to the section of *motor* vascular nerves, this effect of section ought to be supplemented by evidence of the opposite effect, viz., anæmia upon stimulation of the peripheral vagus fibres; an observation which as far as I know has never been made, although the effect of stimulation of the splanchnic nerves shows how easily such anæmia can be observed.

As far as the heart is concerned the vagus is no longer supposed to contain vaso-motor fibres for the coronary arteries although still supposed to contain accelerator fibres for the heart itself. The evidence for such accelerator fibres is mainly based upon the stimulation of the vagus nerve in the frog where, as I have pointed out[1], the true accelerator

[1] *Loc. cit.*

fibres run conjointly with the inhibitory to the heart. In other cases the evidence is given by such observations as those of Panum, Gianuzzi, Traube[1], &c. which show that in weakly-beating hearts stimulation of the vagus may bring about an increase in both rate and strength. Such observations do not prove the presence of accelerator fibres but, as will be pointed out in a later section, illustrate one of the most important effects of the stimulation of the inhibitory cardiac fibres.

Finally we come to the observations of Roy[2] that the vagus contains vaso-motor nerves for the spleen. In his paper he speaks of vaso-motor impulses passing from both vagus and splanchnic nerves to the spleen. His observations are based not on direct observation of the splenic blood-vessels but on the changes of volume in the spleen itself. The diminution of volume therefore which occurs upon stimulation of the vagus may be due to one of two causes, either to contraction of blood-vessels or to contraction of the intrinsic splenic muscles. Roy has pointed out that the spleen is a rhythmically contractile organ, and that such contractions are independent of those rhythmical vascular contractions which show themselves as the well-known Traube-Hering curves; such contractions are therefore in all probability due to the contraction of the splenic muscle fibres, and demonstrate the great diminution of volume which can result in that organ from the action of such muscles. If the vagus therefore is the motor nerve to these muscles—an assumption which is strictly in accordance with one of the main functions of that nerve—the diminution of volume observed by Roy upon its stimulation is fully accounted for without the assumption that it contains vaso-motor fibres.

We may conclude then that no satisfactory evidence has yet been given for the presence of vaso-motor nerves in the roots of the cranial nerves; the same absence of evidence is visible at the other extremity of the central nervous system.

The observations of Eckhard and subsequent observers have proved without doubt that that stream of visceral fibres which passes out of the sacral region and forms the nerves called by them *nervi erigentes* (to which I have given the name of *pelvic splanchnic* nerves) contains motor nerves for the longitudinal muscles of the rectum, bladder and uterus, dilator nerves for the blood-vessels of the erectile tissue of the penis, motor nerves for Houston's muscle, secretory nerves for the prostate

---

[1] Cf. Aubert, Hermann's *Handb. der Physiolog.* Bd. IV. s. 384.

[2] This Journ. Vol. III. p. 203.

gland, inhibitory nerves for the circular muscles of the rectum (Fellner and v. Basch)[1]; but no observer has as yet discovered that it contains a single motor nerve for any blood-vessel. On the other hand, the vaso-motor nerves for the penis are known to run in the *n. pudendus communis,* a branch of the sciatic plexus, and doubtless enter this nerve by means of the grey rami communicantes which pass from the chain of vaso-motor ganglia into the nerves of this plexus.

We have left for consideration the question whether any evidence exists to show that vaso-motor nerves pass out directly in the roots of the cervical, brachial, or sciatic plexuses. There is evidence sufficient to make it highly probable if not certain that the roots of the nerves which supply the extremities do themselves contain nerve fibres which can be called vascular. As however the proofs of their existence make it at the same time probable that they belong to the group of vaso-dilator, i.e. vaso-inhibitory, rather than of vaso-constrictor nerves, I shall postpone their consideration until I reach the section which treats of the inhibitory nerves of the vascular system.

One single fact remains which is applicable to only one kind of animal, viz. that the great auricular nerve of the rabbit contains vaso-motor nerves for the blood-vessels of the ear. I am unable however to find in the literature of the subject that such nerves have been traced into the roots of the cervical auricular nerves; and, seeing the plentiful supply of vaso-motor fibres which pass to the cervical nerves by way of the sup. cerv. ganglion and the *nervi vertebrales,* it is not unreasonable to suppose that the cervical auricular nerves obtain their supply from these two sources and not directly from the cervical region of the cord.

SECTION V. *On the structure and distribution of the viscero-motor nerves.* Pl. III. Fig. 4.

If we pass now to the second group of motor nerves, viz. the viscero-motor, we see at the outset that the nerves of the alimentary canal and its appendages can be divided into two groups, those which supply the longitudinal and circular muscles respectively; of these two divisions it is well known that throughout the greater portion of the alimentary tract the vagus supplies the motor fibres for the latter layer of muscles, causing when stimulated the well-known peristaltic movements. Such peristaltic contractions of the œsophagus, stomach and intestines can be

[1] *Med. Jahrb. d. Ges. d. Aerzte,* Wien, 1883.

excited by vagus stimulation whether the stimulus be applied to the roots of the nerve as they leave the medulla or to the main trunk in any part of its cervical or thoracic course. Such nerves then must form part of the cervico-cranial outflow of visceral nerves and leave the central nervous system in the roots of such nerves as the accessory, vagus and glossopharyngeal. In these roots, as has been already demonstrated, they are recognizable as medullated nerve fibres.

Again, an examination of the vagus nerves at their entrance into the diaphragm shows that they are here composed almost entirely of non-medullated fibres; so overwhelming indeed is the proportion of non-medullated to medullated (whether large or small) in this part of the nerve that no doubt whatever can exist but that the motor nerves of the stomach and intestines must be included among these non-medullated fibres. In other words, nerves which at their origin were medullated have become non-medullated before their arrival at the semilunar ganglia; the conversion therefore must have taken place higher up. An examination of the cervical part of the vagus shows that the non-medullated fibres make their first appearance in large numbers just below the *ganglion trunci vagi;* section of the nerve here shows large quantities of medullated fibres, both large and small, among which quantities of non-medullated fibres are to be seen. Tracing these fibres downwards it is instructive to see how the medullated fibres belonging to each branch group themselves together at the periphery of the main stem before they pass away as a separate branch. In this way groups of medullated fibres pass away in the laryngeal nerves, in the cardiac nerves and in the pulmonary nerves; each successive departure leaving the core of non-medullated nerves more and more free from admixture with medullated, until at last when the pulmonary nerves have gone, the intestinal nerves are left as a mass of non-medullated fibres with a few medullated scattered among them.

It is clear then that the loss of the medulla in some if not all of these viscero-motor nerves takes place in the ganglion trunci vagi. It is easy in this ganglion to isolate nerve cells with a long stretch of non-medullated fibre attached to them, so that it is clear that these nerve cells are connected with the non-medullated fibres.

We obtain therefore so far this proof as to the nature of the motor nerves of the circular muscles of the upper part of the alimentary canal:—

1. They leave the medulla oblongata in the roots of the vagus group of nerves and are therefore medullated.

2. In the thoracic portion of the vagus they are non-medullated.

3. . Non-medullated fibres are in connection with the ganglion cells of the ganglion trunci vagi.

The final link in the chain of evidence which would connect together these three facts is the proof that the cells of the ganglion trunci vagi are connected with the motor nerves in question.

Such a connection is easily proved by the method of degeneration, as is seen from the following experiments on the crocodile.

The roots of the vagus nerve of the crocodile pass into a large ganglion which, according to Fischer[1], is made up of the three ganglia, the *ganglion jugulare vagi, ganglion jugulare glossopharyngei* and *ganglion petrosum glossopharyngei.* From this ganglion the laryngo-pharyngeal nerve and the vagus pass out separately. The vagus passes down the neck and does not form a second ganglion until after its entrance into the thoracic cavity. This second ganglion is the *ganglion trunci vagi;* so that in this animal the whole of the cervical portion of the vagus separates its two ganglia. It is therefore easy to cut out a portion of the cervical vagus and so to isolate the *ganglion trunci vagi* from the central nervous system ; the functions of the isolated ganglion can then be determined after the nerves passing to it have been allowed to degenerate.

In young specimens of *Crocodilus biporcatus*[2] this ganglion forms a well-defined oval mass on the main trunk of the vagus just at its entrance into the thorax; the vagus continues as an unbranched nerve for a short distance below the ganglion, and then begins to divide into its intestinal, cardiac and pulmonary branches. The only branch which is given off directly from the ganglion is an undivided fine nerve which passes directly to the heart, entering the heart with the aortic vessels and never passing to the venous side. This branch, which is always present and conspicuous, corresponds possibly, as pointed out in a previous paper[3], to the n. depressor. No other communication whatever exists with this ganglion, so that its isolation from the central nervous system is of necessity complete as soon as the cervical vagus is cut.

In *Alligator mississippiensis* this ganglion lies deeper and, as is seen in one of the figures which illustrate the paper already referred to[4], the nerve divides immediately at the lower border of the ganglion.

---

[1] "Die Gehirnnerven der Saurier." *Abhandl. d. naturwiss. Vereins in Hamburg,* 1852.

[2] I again desire here to express my thanks to Sir Joseph Fayrer and to Dr Kinsey of Colombo, Ceylon, for their kindness in obtaining these crocodiles for me.

[3] Gaskell and Gadow. This Journ. Vol. v. p. 362.

[4] This Journ. Vol. v. Pl. xi. Fig. I.

I have cut a piece out of the cervical portion of one or both vagi nerves in eleven young crocodiles and in two large alligators from 4 to 5 ft. long. In all cases a piece of the nerve from half an inch to an inch in length was cut away, and in most cases the peripheral end of the nerve was enclosed in the stitches which united the skin wound. The following table shows the date of the sections and the time after the section when the animal was killed.

Crocodilus biporc.

	L. Vagus cut	R. Vagus cut	Animal killed	Length of time after sect. of	
				L. Vagus	R. Vagus
1.	Mar. 10, 1884	not cut	April 10	31 days	
2.	Mar. 10, 1884	not cut	April 28	49 days	
3.	April 25, 1884	March 26	May 20	25 days	55 days
4.	Mar. 24, 1884	May 3	June 3	71 days	31 days
5.	not cut	March 31	June 19		80 days
6.	Mar. 24, 1884	April 25	July 18	116 days	84 days
7.	May 27, 1884	March 31	Oct. 8	134 days	191 days
8.	May 3, 1884	March 26	Found dead on Nov. 25	206 days	244 days
9.	not cut	Oct. 29, 1884			
10.	not cut	Oct. 29, 1884	still alive		
11.	not cut	Oct. 29, 1884			

Alligator mississipp.

	L. Vagus cut	R. Vagus cut	Animal killed	Length of time
1.	Oct. 1, 1884	not cut	May 4, 1885	215 days
2.	Oct. 1, 1884	not cut	July 28, 1885	300 days

In all cases the wound in the neck healed perfectly, no difficulty whatever was experienced in keeping the animals alive, and the only death which occurred took place more than 200 days after the removal of a large portion of both vagus nerves. As I do not propose in this paper to discuss the reason of death after section of both vagi, I will simply state that in these animals such section does not interfere with the respiration more than a day or two after section of the second nerve; the lungs present a normal appearance after death. Death does not occur owing to the absence of food, for not only do the animals eat, but food is found partially digested in the stomach and in the intestines, and well-formed fæces are seen in the rectum, even in those cases where the two nerves had been cut longest. Yet the animals do die of starvation, for the longer the time which has elapsed after the double section the more

complete is the disappearance of the fat body, the more marked are the
signs of inanition in all the thoracic and abdominal organs.

In all cases the inhibitory power of the vagus on the heart
disappeared completely; no difference was found in this respect whether
the nerve was tested above or below the ganglion trunci, no effect could
be produced by the stimulation of the cardiac fibres below the ganglion
any more than by stimulation of the cervical vagus above. Also it
should be remarked that in the intact crocodile both right and left
nerves cause absolute and long continued standstill even with a weak
stimulus. Clearly then the cardiac inhibitory fibres of the vagus
degenerate right through this ganglion and are not therefore in con-
nection with its ganglion cells.

In order to estimate the influence of the ganglion upon the motor
nerves of the œsophagus and stomach, we must in the first place know
the effect of stimulation of the intact nerve both above and below the
ganglion. In the above list we see that in three of the young crocodiles
the nerve was cut only on one side, so that in these three animals the
effect of stimulation of the freshly-cut nerve could be examined; in ad-
dition I sacrificed on May 31, 1884, a healthy intact crocodile for this
express purpose. Further we have the right nerves of the two alli-
gators for comparison.

In all the crocodiles I noticed the same effect of stimulation of the
peripheral ends of either right or left vagus whether above or below the
ganglion, viz. a strong peristaltic contraction of the whole œsophagus
extending throughout the cervical and thoracic portions into the stomach
and followed by contraction of the stomach itself; the only variation
observed was in the case of the crocodile killed on June 19, in which the
contraction of the œsophagus caused by stimulation of the L. vagus
extended only to the middle of the cervical region and not therefore as
high as in the other cases.

In the two alligators stimulation of the peripheral end of the cervical
portion of the vagus on the uninjured side caused a marked contraction
of the thoracic portion of the œsophagus and of the stomach, but did not
produce any effect upon the cervical portion. On the other hand in one
of these two animals where the medulla oblongata was intact, and both
vagi had been cut, a series of rhythmical spontaneous peristaltic con-
tractions were observed, which passed down the whole of the cervical
portion of the œsophagus and ceased abruptly at the junction of the
cervical and thoracic portions, at in fact the same place which marked
the commencement of the contraction upon stimulation of the peripheral

end of the vagus. These contractions ceased after the destruction of the medulla oblongata. In the alligator then the motor nerves for the cervical portion of the œsophagus pass directly to it probably by way of the large conjoint vagus and glossopharyngeal ganglion and the pharyngo-laryngeal nerve, while those for the thoracic portion and the stomach and intestines pass through the ganglion trunci vagi. We see also in this observation the complement of Mosso's experiment. He showed that a peristaltic contraction could be excited from the centre and pass along the whole œsophagus even when the œsophagus was divided. The above observation shows that such peristaltic contractions cannot pass along an intact œsophagus unless the nerves are intact.

In the crocodile it would appear that some at all events of the motor nerves for the cervical portion of the œsophagus passed through the ganglion trunci vagi on their way to that portion of the œsophagus.

The effect of section of the vagus in the cervical region with subsequent degeneration of its fibres is well marked in this series of experiments. In all cases the cervical portion of the œsophagus remained absolutely quiescent, whether the degenerated nerve was stimulated above or below the ganglion trunci. In all cases except in one instance stimulation of the degenerated nerve above the ganglion produced not the slightest effect upon any portion of the œsophagus or stomach. In all cases except one, stimulation of the nerve below the ganglion caused marked peristaltic contraction of the thoracic portion of the œsophagus and stomach. This contraction differed from that of the intact nerve in that the contraction produced by the same strength of stimulus was rather weaker, and the latent period was longer. Its marked characteristic was the abrupt line of demarcation between the contracted and uncontracted portion. Sometimes the peristaltic movement spread from above downwards, sometimes from below upwards; in both cases it never overstepped the limit of the thoracic portion; even when the contraction was strong it ceased abruptly here, forming a circular indentation at the junction of the cervical and thoracic portions.

These experiments prove clearly that those fibres which pass down the cervical portion of the vagus to innervate the cervical portion of the œsophagus, like the inhibitory cardiac fibres, degenerate after section of the nerve, while those fibres which innervate the thoracic portion of the œsophagus, the stomach and, in all probability, the intestines degenerate only in that portion which is above the ganglion but not in that portion below the ganglion.

Clearly from these facts the motor nerves for the upper portion of

the œsophagus and the inhibitory fibres for the heart have no connection
with the nerve cells of the ganglion trunci vagi, while the motor nerves
for the rest of the œsophagus and the upper portion of the remainder of
the alimentary canal are in connection with the cells of that ganglion—
a connection by which the motor nerve fibres proceeding peripherally
from the ganglion are prevented from degeneration, but not the motor
fibres which pass to the ganglion.

Further, it may be mentioned at the same time that this nutritive
power of the ganglion cell over the peripheral nerve fibre is not associated
with any recovery of the functional activity of the motor fibre in conse-
quence of the cell acting as a reflex centre.

Both in the intact and in the degenerated nerve I have carefully
tried the effect of stimulation of the central end of various intestinal
branches such as those passing over the stomach, also of the cardiac and
pulmonary branches, the ganglion having been previously isolated from
the central nervous system by section of the vagus in the neck.

In no case have I seen the slightest indication of any reflex action
through the ganglion; in no part of the œsophagus or stomach was it
possible to detect any trace of movement upon stimulation of these
nerves: in other words, although experiment proves that the
motor nerves of the thoracic portion of the oesophagus are
connected with the nerve cells of this ganglion, yet it is im-
possible to excite them reflexly through those nerve cells.

Putting together the knowledge gained up to this point we can
say:—

The viscero-motor nerves upon which the peristaltic con-
traction of the thoracic portion of the oesophagus, stomach
and intestines depends, leave the central nervous system in
the outflow of fine medullated visceral nerves which occurs
in the upper part of the cervical region, and pass by way of
the rami viscerales of the accessory and vagus nerves to
the ganglion trunci vagi, where they become non-medul-
lated.

These viscero-motor nerves therefore resemble in their structure and
in the method of their distribution the vaso-motor nerves already de-
scribed.

In addition we see further that the nerve cells of the proximal
ganglia are not only concerned in the conversion of the medullated
motor nerves into non-medullated, but also possess a nutritive power
over the fibres which pass from them peripherally.

The difference between the effect on the blood-vessels of the ear after section of the cervical sympathetic and after removal of the sup. cervic. ganglion; the persistence of vaso-motor and secretory action in fibres passing from the sup. cervical ganglion to the submaxillary gland after complete degeneration of these fibres in the cervical sympathetic (as noticed by Langley[1]), all point to the conclusion that such nutritive power is a universal property of the ganglion cells found on all visceral nerves.

If we take the viscero-motor nerves of the vagus as the type of such nerves we should expect to find that in all cases they passed out of the central nervous system in the rami viscerales, and lost their medulla in ganglia which are homologous to the ganglion trunci vagi. Two considerations however must be borne in mind; firstly, the motor nerve fibres of the vagus which we have been dealing with are those which supply the circular layer of muscles; secondly, the exact position of the ganglion trunci vagi has not been established beyond dispute; so that in any endeavour to establish the course and anatomical relations of viscero-motor nerves in parts which are free from the influence of the vagus we can only expect to find that the fibres which supply circular muscles possess characters similar to those described above; the nerves which supply the longitudinal muscles may reasonably form another group presenting different characteristics.

Conversely, if we can fully trace out the course and relations of those spinal nerves which supply the circular muscles, then further light will be thrown upon the position of the ganglion trunci vagi, and therefore upon the homologies of the vagus and spinal nerves.

In the hind-gut and its appendages we find a viscero-motor nerve-supply which arises from the lower part of the spinal cord and is entirely free from the admixture with vagus fibres; these do not reach to this part of the intestine.

The motor fibres therefore which supply the rectum, bladder and uterus must, if their course can be traced, afford the information required.

An examination of the literature of the subject brings out clearly the remarkable similarity in the innervation of these three organs; in all the motor nerve-supply is double and, according to the language of the day, is divided into a cerebro-spinal and sympathetic set of nerves. The cerebro-spinal nerves pass to the hypogastric plexus and from thence to the rectum, bladder and uterus by those visceral branches of

---

[1] This Journ. Vol. vi. p. 87.

the 2nd and 3rd sacral nerves which are known by the name of *nervi erigentes*, i.e. they pass out of the central nervous system in the sacral stream of visceral nerves and reach their destination by way of the pelvic splanchnics.

The sympathetic nerves on the other hand pass to the inferior mesenteric ganglion along the rami efferentes of that ganglion and from thence along the hypogastric nerves to the hypogastric plexus; they therefore leave the central nervous system in the thoracic stream of visceral nerves.

The motor actions of these two sets of nerves distinctly differ from each other and the difference appears to be of the same kind in all the three organs in question. Undoubtedly the pelvic splanchnics supply the longitudinal muscles of the rectum, the longitudinal muscles of the bladder or *detrusor urinæ,* and apparently the longitudinal muscles of the uterus. Equally undoubtedly a true peristaltic contraction of the rectum, i.e. a contraction of circular muscles, is caused by stimulation of the hypogastric nerves or of the lower abdominal splanchnics. Fellner[1] in v. Basch's laboratory has established this difference in the action of the two sets of nerves for the rectum of the dog.

I myself have examined this question both in the dog and frog and entirely endorse the conclusion of Fellner. In the dog, even after death, the pulling down of the rectum owing to the contraction of the longitudinal fibres when the pelvic splanchnic nerve is stimulated is easy to observe, while upon stimulation of the hypogastric nerve no direct downward pull takes place but, instead, a distinct peristaltic movement is seen.

It is especially noteworthy that the same differences in nerve supply exist in the frog as in the dog; the so-called sympathetic motor supply for the bladder and rectum passes out of the spinal cord in the rami communicantes to the sympathetic ganglia and from thence along the hypogastric nerves to their destination; the ramus communicans chiefly involved appears to be that of the 7th nerve. The so-called cerebro-spinal supply passes out of the roots of the 8th and 9th nerves into the sciatic plexus and leaves this plexus in the shape of a fine white nerve which passes to the bladder and rectum; in fact the origin and course of this nerve is identical with that of the so-called nervi erigentes (pelvic splanchnics) in mammals. The action of these two nerves in the frog is also precisely the same as in the mammal. Stimulation of the pelvic splanchnic nerve causes a marked pulling down of the rectum and a

[1] *Op. cit.*

strong contraction of the bladder owing to the shortening of the fibres of the detrusor urinæ; on the other hand, upon stimulation of the ramus communicans of the 7th nerve, no downward movement of the rectum takes place, but a contraction of the circular muscles which can be observed directly by means of a lens.

The nature of the contraction of the bladder which takes place when the hypogastric nerve or the abdominal splanchnics are stimulated is not so clear. The main appearance (and this applies equally to the frog) is, as noticed by Gianuzzi[1], a much weaker contraction with these nerves than with the other set. As yet I have not been able to convince myself whether this weakness of effect is due to a diminished action of the longitudinal muscles of the detrusor urinæ or, as is more probable, to the action of the more circularly arranged muscle fibres which, although contracting fully, are incapable of producing much visible effect upon the fundus of the organ.

According to the researches of Körner, Röhrig[2] and others, the uterus is supplied with two sets of nerves, the *nervi uterini* which reach the uterus by way of the main sympathetic and hypogastric nerves and therefore belong to the abdominal splanchnics, and the *nervi uterini sacrales* which pass free from the main sympathetic chain and belong to the pelvic splanchnics. Further, according to v. Basch and Hofmann[3], stimulation of the hypogastric nerves causes a contraction of the circular muscles of the uterus, while stimulation of the cerebro-spinal nerves causes the longitudinal muscles to contract.

From what has been said it is clear that the viscero-motor fibres of the hind-gut and its appendages, homologous with those fibres of the vagus which cause peristaltic contraction of the œsophagus, stomach and intestines, leave the spinal cord in the thoracic rather than in the sacral outflow of visceral nerves. At present it is impossible to say -with certainty in which group of ganglia they lose their medulla; we do not even know whether they leave the spinal cord in anterior or in posterior roots, and until this question is answered it is useless to endeavour to map out their course further than I have already done.

With respect to the other group of viscero-motor nerves, those which innervate the longitudinal muscles of the hind-gut and its appendages, we can speak more confidently; they most certainly pass out of the cord in the anterior roots. Budge[4] describes the motor nerves of the *detrusor urinæ* in the dog as passing out in the 1st, 2nd and 3rd sacral nerves. I

---

[1] *Journ. d. l. physiol.* VI. p. 22.　　[2] Henle, *Anat. d. Menschen.*
[3] *Wiener med. Jahrb.* 1877.　　[4] Pflüger's *Archiv*, Bd. VI. s. 306.

myself have found that these same nerves in the frog, as well as those which supply the longitudinal muscles of the rectum, pass out in the anterior roots of the 8th and 9th nerves.

Seeing then that these anterior roots contain only medullated fibres and have no possibility of communicating with ganglion cells until they arrive at the hypogastric plexus it follows that such nerves must either lose their medulla in these ganglia or else continue as medullated nerves to the longitudinal muscles themselves. It must be left to future investigation to determine which of these two possibilities is true.

SECTION VI. *On the structure and distribution of the vaso-inhibitory (vaso-dilator and cardio-inhibitory) nerves.* Pl. III. Fig. 5.

The presence of special vaso-dilator nerves for the blood-vessels of every part of the body is an accepted article of faith for almost all physiologists of the present day. Owing however to the fact that in most instances such nerves are found mixed up with the vaso-motor nerves the evidence upon which their existence is based is in the majority of cases indirect rather than direct. Fortunately we possess among the vaso-inhibitory nerves a few examples, the separate existence of which is beyond dispute. In these cases these nerves run separately from the vaso-motor so that an examination of their structure and distribution may fairly be expected to give indications of general laws, if such exist, which may afterwards be tested in the case of the other vaso-inhibitory nerves. The nerves in question are *par excellence* the inhibitory fibres of the heart, the vaso-dilators contained in the chorda tympani and small petrosal nerves, and the nervi erigentes.

Naturally, as might be expected from what has already been proved about the course of the vaso-motor nerves, all these instances of undoubted vaso-inhibitory nerve fibres which run a separate course distinct from vaso-motor fibres are found exclusively in connection with the cervico-cranial and sacral outflows of visceral nerves.

The cardiac fibres of the vagus constitute the recognized type of inhibitory nerves; and fortunately these fibres can be followed from their origin to their termination. In all animals which I have examined these pass into the heart as medullated fibres. The examination of them by sections and teazing after they have left the vagus and before they have entered the heart shows, in the case of the rabbit where they can be obtained free from admixture with other nerves, that they form bundles of medullated fibres very uniform in

size and all of the finest calibre. They belong in fact in size to the group of nerve fibres which we have found to be associated with the several outbursts of visceral nerves. As already mentioned fibres of the same size are found in the roots of the accessory and vagus nerves, in roots which we know to contain the inhibitory fibres of the heart.

Further, as already mentioned, the degenerative experiments which I have described in connection with the vagus nerve of the crocodile prove conclusively that these heart nerves have no connection with the ganglion trunci vagi.

It follows clearly that they leave the central nervous system in the rami viscerales of the vagus and accessory nerves and retain the same fine medullated nerve structure until they reach the heart. Here undoubtedly they enter into connection with ganglion cells, and judging from the heart of the frog—where as is well known the medullated fibres of the nerves of the auricular septum enter into the auriculo-ventricular ganglia (or Bidder's ganglia) and cannot be traced further, the nerves proceeding from these ganglia over the ventricle being almost entirely composed of non-medullated fibres—we may conclude that they lose their medulla in these ganglion cells.

Such a course can be contrasted with that of the motor group of cardiac nerves as follows :—

The vaso-inhibitory cardiac nerves leave the central nervous system among the fine medullated nerves which characterize the formation of the cervico-cranial rami viscerales, pass without altering their character into the distal ganglia where they lose their medulla and continue onwards as non-medullated fibres.

The vaso-motor cardiac nerves on the other hand leave the central nervous system among the fine medullated nerves which characterize the formation of the thoracic rami viscerales, pass without altering their character into the proximal ganglia, where they lose their medulla and continue onwards as non-medullated fibres.

Again, an examination of the nerves mentioned above as containing undoubted vaso-dilator fibres, such as the chorda tympani and the nervi erigentes, demonstrates the preponderance of medullated fibres throughout the whole course of these nerves. Among these medullated fibres those of the finest size are present in large quantities. Such fibres most certainly remain unaltered in their structure close up to their termination in the tissues. For instance, the structure of the chorda tympani remains the same as far as the presence of such fibres is concerned up

to its entrance into the submaxillary ganglion; so too the same fine fibres pass in the nervi erigentes unaltered in character up to the ganglia of the hypogastric plexus. The probability is therefore exceedingly great that the vaso-dilator nerves in these two instances pass to these distal ganglia without any alteration of their structure; whether they lose their medulla in these ganglia or pass still further into the organs they supply and become non-medullated in connection with ganglion cells of the same character as the ·erminal ganglia in the heart can only be settled by further investigation. In favour of the latter proposition is the fact that the majority of the medullated fibres of the chorda tympani, which supply the submaxillary gland, pass over the submaxillary ganglion without entering into communication with it.

If therefore we include the submaxillary ganglion and the ganglia in the submaxillary gland itself as well as the hypogastric ganglia and those which are found nearer the corpora cavernosa, in the common term of distal ganglia, we can include both the cardiac inhibitory nerves and these undoubted vaso-dilator nerves under the same description, and say that "They leave the central nervous system among the fine medullated nerves which help to form the cervico-cranial and sacral rami viscerales and pass without altering their character into the distal ganglia."

The evidence then of the best known examples of nerves containing vaso-dilator fibres is in favour of the supposition that all such nerves conform to the type of the cardiac inhibitory nerves, in so far as the size of their fibres, their direct connection with the distal ganglia and their avoidance of the chain of vaso-motor ganglia is concerned.

The evidence for vaso-dilator nerves in other parts of the body is largely based upon experiments conducted upon the blood-vessels of the lower extremity and my experiments upon the circulation through the mylohyoid muscle of the frog. In these cases the vaso-dilator fibres cannot be isolated in the course of the peripheral nerve; we are therefore driven to their origin from the central nervous system in our attempts to find out their anatomical relations. The experiments of Schiff, Stricker, Luchsinger, Puelma and Luchsinger[1] all point to the roots of the sciatic nerves themselves as being the paths by which the vaso-dilators for the foot leave the central nervous system, and Stricker goes further still and says that they pass out in the posterior roots of these nerves; until however we possess more definite information on this subject than we have at present it is inadvisable to

[1] Cf. Aubert, Hermann's *Handb. d. Physiolog.* Bd. IV.

attempt to compare the paths of these nerves with those which are known to leave the central nervous system in the roots of certain cranial nerves. On the other hand, we cannot argue from the path of such nerves in the roots of the vagus and chorda tympani to their path in the roots of spinal nerves, until we know more fully to what portions of the spinal nerve roots the roots of such a nerve as the vagus correspond. In an appendix to this paper I propose to point out certain considerations which may materially help to guide us in the solution of this question.

SECTION VII.   *On the structure and distribution of the viscero-inhibitory nerves.*   Pl. III. Fig. 3.

At present, unfortunately, our knowledge of the course and relations of the inhibitory nerves of the visceral muscles is so very imperfect, that we can hardly hope to deduce any general law from the evidence in our possession. I propose therefore to discuss simply the characteristics of those viscero-inhibitory nerves which are known to pass in the splanchnics, and then to examine the nature of any other nerve fibres which are known to follow a corresponding course.

Three kinds of nerve fibres innervating visceral tissues are said to pass out of the central nervous system by way of anterior roots in the thoracic region, viz. vaso-motor nerves, the viscero-inhibitory nerves of the splanchnics, and the glandular nerves which supply the submaxillary, parotid and other glands. All these nerves pass into the sympathetic system from anterior roots and reach that system therefore as me-dullated nerve fibres.

The vaso-motor portion of those fibres have been already traced into the lateral or vaso-motor ganglia, while the medullated fibres, which constitute the major portion of the splanchnic nerves, have been seen to pass direct to the semilunar and other ganglia of the collateral chain without entering into connection with the vaso-motor ganglia.

An examination of the structure of the splanchnic nerves shows that they are composed mainly of medullated fibres, the non-medullated amounting in man, according to Rüdinger[1], to a bare fifth part of the whole number of fibres. The medullated fibres all belong to the group of smallest fibres with the exception of a few isolated larger ones. The contrast between the structure of the splanchnics and of the vagi nerves on their way to enter the semilunar ganglia is most striking; in the

[1] Cf. Henle, *Anatom. d. Menschen.*

one case a mass of fine medullated nerves with comparatively few non-medullated among them, in the other a mass of non-medullated among which a few fine medullated are to be seen.

Of the three components of the splanchnics the non-medullated nerve fibres alone can be traced into the ganglia of the lateral chain, both large and fine medullated pass direct from the nerve roots to the collateral ganglia.

Clearly, from what has already been proved, the vaso-motor nerves which are known to run in the splanchnics must in all probability be found in these non-medullated fibres; it follows that the viscero-inhibitory nerves must be included among the medullated fibres, for it is impossible to conceive that the large amount of muscular tissue represented by the walls of the alimentary canal and of the abdominal blood-vessels conjointly should receive such an important portion of its nerve supply from the comparatively few non-medullated fibres found in the splanchnics. Also the contrast in structure between the vagus and splanchnics nerves points strongly to the conclusion that the viscero-inhibitory nerves must be included among the medullated fibres in this part of their course; for, if the visceral muscles are supplied with inhibitory nerves as freely as with motor nerves, then the same argument will apply to the preponderance of medullated fibres in the splanchnics as to that of non-medullated in the vagus; so that we are led to the conclusion that the motor fibres of the circular muscles of the stomach and intestines lose their medulla before they reach the semilunar ganglia while the inhibitory are still medullated at their entrance into those ganglia.

As already mentioned we cannot trace these fine medullated fibres further, at all events in distinct bundles. An enormous number of non-medullated fibres streams out from these large ganglia to the intestines, stomach, liver, kidney, spleen, &c., in the midst of which the large medullated fibres of the abdominal splanchnics can be easily traced. The smallest medullated fibres occur very sparingly isolated among the grey, and are no longer traceable in bundles.

Seeing the numbers of such fibres which pass into the collateral ganglia by the rami efferentes and the scarcity of them in the rami peripherales it is practically certain that some of them lose their medulla in these ganglia.

At present it is only probable, not certain, that the viscero-inhibitory nerves of the circular muscles are among those which become non-medullated in these ganglia; it is just possible that they proceed

further to the terminal ganglia before losing their medulla. In either case we can say that these viscero-inhibitory nerves, like the vaso-inhibitory nerves, differ from the corresponding motor nerves in that they proceed to the distal ganglia before becoming non-medullated, while the latter lose their medulla in the proximal ganglia.

On the assumption that these fibres of the splanchnic are typical of the nerves of this group we might describe the group as follows:

The inhibitory nerves of the circular muscles of the alimentary canal and its appendages leave the central nervous system in the anterior roots and pass out among the fine medullated fibres of the rami viscerales into the distal ganglia without communication with the proximal ganglia.

At present the evidence for the existence of other members of this group of nerves is too fragmentary and uncertain to enable us to follow out their course. We can, I think, say no more than this that the experiments of Fellner and v. Basch, of Kronecker and his pupils, point to their distribution not being confined to the thoracic outflow of visceral nerves. It is possible and indeed probable, as described by Fellner[1], that they pass to the circular muscles of the hind-gut and its appendages along with the motor nerves of the longitudinal muscles, and therefore follow the same course in connection with the sacral visceral outflow as with the thoracic.

Conclusions.

In the foregoing sections I have considered only the nerves which supply the muscles of the vascular and visceral systems and have shown that all such nerves have certain common histological characteristics, while nerves of the same function possess in addition a well defined anatomical course.

They are all composed of medullated fibres of the finest size (a fact originally noticed by Bidder and Volkmann as characteristic of the sympathetic nervous system) which lose their medulla and become non-medullated before they reach their destination.

One of the functions of the ganglia with which they are in connection is to effect this conversion of medullated into non-medullated fibres.

A commencement has been made in defining the anatomical course

---

[1] *Op. cit.*

of these nerves by tracing for each kind of nerve the characteristic small
medullated fibres from the central nervous system into the special group
of ganglia in which the loss of the medulla takes place.

Although this anatomical course cannot at present be defined in
every case to its fullest extent, yet sufficient evidence has been given to
warrant the conclusion that the vascular and visceral muscles are
throughout supplied by two kinds of nerve fibres of opposite function, the
one motor and the other inhibitory; and that further these two kinds of
nerve fibres reach the muscle by separate distinct anatomical paths, the
difference of path consisting in a difference of origin from the central
nervous system combined with the fact that the inhibitory nerves lose
their medulla in more distant ganglia than the corresponding motor
nerves.

In addition the ganglia have been shown to possess a nutritive
power over the nerves which pass from them to the periphery.

A third function of these ganglia remains to be noticed, viz. the
increase in the number of nerve fibres which occurs simultaneously with
the loss of the medulla.

It is generally acknowledged, since the publication of Bidder and
Volkmann's[1] paper, that an increase of nerve fibres takes place at the
various ganglia. The nature of such increase is easily seen by the mere
inspection of the nerves which are in connection with such a ganglion as
the superior cervical; the number of non-medullated fibres which pass
out of it to proceed peripherally along the internal and external carotid
nerves and along the peripheral grey rami communicantes of the upper
cervical and lower cranial nerves is immensely greater than all the fibres
both medullated and non-medullated which pass to it from the central
nervous system along the cervical splanchnic (cervical sympathetic)
nerve. So too the masses of non-medullated fibres which leave the
semi-lunar ganglia to be distributed to the stomach, liver, intestines &c.
are very much greater than all the fibres contained in the rami efferentes
of these ganglia. It is only necessary to picture to oneself the number
of fine medullated nerves contained in the various nerve roots, in
comparison with the number of non-medullated fibres which pass out of
the various ganglia of the body, to see what a great increase of nerve
fibres must have taken place in the course of the nerves between the
central nervous system and the periphery. Doubtless such increase is
partly to be accounted for by the direct division of non-medullated

---

[1] *Die Selbstständigkeit d. Sympath. Nervensystems,* 1842.

nerve fibres. Such division however takes place chiefly in connection
with the passage of the nerve through a ganglion.

Hitherto investigators relying upon histological examination only
have tended strongly to attribute such increase at a ganglion to the
presence of new fibres, which have their birth in the cells of the ganglion,
without attempting to explain any causal connection between such fibres
and those which connect the ganglion in question with the central
nervous system. In the face however of the physiological facts given
above such a causal connection is absolutely necessary, and it seems to
me that the negative evidence of histology possesses no weight at all
against the positive evidence of physiology that such a connection must
take place.

I picture to myself the anatomical arrangements of these visceral
nerves somewhat as follows.

Each nerve fibre leaves the central nervous system as a fine
medullated nerve fibre which passes directly into its appropriate ganglion,
and there in consequence of communication with one or more of the
ganglion cells loses its medulla and passes out not as a single non-
medullated fibre but as a group of non-medullated fibres. Such ganglion
cells not only assist in the conversion of a single nerve fibre into a group
of fibres but at the same time are centres for the members of the group
in so far as they possess a nutritive power over them; they are not
however centres in the sense of being capable of reflexly setting these
fibres into activity; a conclusion which is self evident if each nerve cell
is connected only with nerve fibres possessing the same function.

The extension of the nutritive power of the ganglion over the nerve
fibres which proceed from it to the end organs of those nerve fibres, i. e.
the tissues which they supply, would go far to explain the beneficial
effect upon the tissues, such as the recovery of tone, which has been
often supposed to depend upon the continuance of the connection
between the tissue and one or other group of ganglion cells; while at the
same time the impossibility of any reflex action taking place through
them prevents them from supplying the place of the central nervous
system when no longer in connection with that system.

The difference in size between the motor nerves of the visceral and
vascular muscles and those of ordinary skeletal muscles, which has been
clearly proved in the foregoing pages, leads directly to the conclusion
that it may be possible in all cases to connect together the size of the
nerve fibre with the nature of the tissue which it supplies.

Doubtless valuable information on this question will be afforded by

thorough investigation of the glandular nerves; such investigation I have as yet only commenced, so that it would be premature at present to draw any conclusion from the size of their fibres.

We can however, without leaving the muscular system, obtain further evidence upon this point; for in the muscular tissue of the tongue we possess an example of muscular structure which is intermediate between that of ordinary skeletal muscles and of involuntary muscles, though on the whole more nearly approaching the former than the latter type.

In Pl. I., Fig. 4, I give a section of one of the roots of the hypoglossal nerve.

The comparison of this figure with the large fibred root of the spinal accessory, Pl. I., Fig. 2, or the anterior root of the 1st or other cervical nerve, shows how striking is the difference in size between even the largest fibres of the hypoglossal and those of its neighbouring motor nerves.

The large fibres of the spinal accessory vary from $14.4\,\mu$ to $18\,\mu$; those of the anterior root of the 1st cervical nerve measure $16\,\mu$ and upwards, while the largest fibres of the hypoglossal vary between $7.2\,\mu$ and $10.8\,\mu$.

These latter sizes are characteristic of the majority of the large fibres of the vagus roots as well as of the hypoglossal, while they are comparatively rare in the anterior roots of all spinal nerves.

Coincidently then with the feature that in structure and physiological behaviour the tongue muscles are intermediate between the skeletal and visceral muscles we find their motor fibres ($7.2\,\mu$ to $10.8\,\mu$) intermediate in size between the fine fibres ($1.8\,\mu$ to $3.6\,\mu$) of the motor nerves of the vascular and visceral system and the large fibres ($14.4\,\mu$ to $19\,\mu$ and upwards) which form the motor nerves of ordinary skeletal muscles.

Clearly also Schwalbe's[1] hypothesis that the size of the nerve fibre depends on the length of it is untenable; his measurements are however valuable, especially those which deal with the nerves of man, for his observations show the strong probability that the conclusions which I have arrived at on the relation between the structure and function of the nerves in the dog are applicable word for word to those of man.

In both cases the anterior roots of the first nine spinal nerves are devoid of the smallest medullated fibres; bundles of the finest fibres, varying according to Schwalbe between $1.8\,\mu$ and $2.7\,\mu$, make their

---

[1] *Ueber die Kaliber Verhältnisse der Nervenfasern.* Liepzig, 1882.

appearance for the first time in the anterior root of the 2nd thoracic
nerve. Here then in man as in the dog is the commencement of the
thoracic outflow of visceral nerves.

Again, the fact that involuntary muscles are supplied with two
efferent nerves which differ not only in function but also in their
anatomical course leads naturally to the conception that a similar double
nerve supply exists for all tissues.

In the case of glandular tissue such a double supply has been proved
to exist for the submaxillary, parotid and lachrymal glands; and it is a
significant fact that in these three cases the course of the two sets of
nerves is very similar to that of the two nerves which supply the blood-
vessels of the same parts.

Thus the so-called sympathetic nerve supply for these glands passes
out among the visceral nerves of the thoracic outflow in the anterior
roots along with the vasomotor fibres of their blood-vessels, and reaches
the glands by way of the cervical splanchnic (cervical sympathetic)
nerves and superior cervical ganglion; the so-called cerebro-spinal nerve
supply passes out from the central nervous system in the rami viscerales
of the cranial nerves along with the vaso-dilator nerves of the same
blood-vessels.

Coincidently with this difference of anatomical path we find a differ-
ence of physiological action which is sufficiently well marked to warrant
the conclusion that these glands are supplied with two kinds of nerves
which are physiologically as well as anatomically distinct.

Further we possess in the sphincter muscle of the iris a muscular
structure which cannot be included in the same group as any of the
muscles which have been as yet described.

Although an unstriped and apparently involuntary muscle in mam-
mals, it is a striped and voluntary muscle in birds. In both classes it
receives its motor nerve supply from the 3rd or oculo-motor nerve ; in
both the size of the pupil is dependent upon the extent of its contraction
or relaxation.

At present these motor fibres contained in the 3rd nerve are the only
efferent fibres which are recognized as supplying the sphincter of the
iris; we find however another set of fibres whose action is an antagonistic
one causing always dilation of the pupil, never constriction ; these fibres
are supposed to be the motor nerves of an antagonistic muscle, the so-
called *m. dilator pupillæ.*

These nerves pass to the iris in a path separate from that of the
motor nerves of the sphincter muscles, viz. along the cervical sympathetic,

and their stimulation always causes a most evident dilatation of the
pupil; if this action is due simply to contraction of dilator muscle fibres
it is clear that such fibres must form as important and manifest a con-
stituent of the structure of the iris as the antagonistic circular fibres of
the sphincter: nay more, in order to perform the task demanded of them
the arrangement of their fibres must be even more perfect, uniform and
symmetrical than those of the sphincter, for it is easier to lessen an aper-
ture by the contraction of a circular ring and still keep it circular than
to open that aperture without its losing its circular shape by the con-
traction of fibres arranged radially.

If therefore these dilator nerves are motor to a *m. dilator pupillæ*
the existence of that muscle ought to be at least as evident as that of
the sphincter itself.

We find however in the literature of the subject that, so far from
such a muscle being universally recognized, the very existence of any
dilator muscle fibres at all is called in question. Of late years an
increasing number of observers have taken the side of Grünhagen and
spoken in decisive terms against the muscular character of the radial
fibres in the posterior limiting membrane of the iris. In the most recent
paper which I have seen Koganei[1] discusses the whole structure of the
iris in a large number of different animals, and concludes definitely, that
the posterior limiting membrane is in no case muscular, and that
therefore the dilator muscle is to be found in certain muscular fibres
which pass in a radial direction out from among the fibres of the sphincter
towards the ciliary margin of the iris. At the same time he confesses
that such fibres are strongly developed only in the otter and in birds,
while in man and all other animals examined by him no sign of their
existence could be found except in the rabbit, where indications of them
were present.

Clearly then, whatever may be their function in the otter, such
fibres are inadequate to explain the action of the dilator nerves of the
pupil in other mammals.

For my own part I cannot see the urgent necessity for a special
m. dilator pupillæ; variations in the extent of the contraction or
relaxation of the sphincter are quite sufficient to account for all the
differences in the size of the pupil, if only the radial fibres of the iris
possess, as Grünhagen thinks they do, a sufficient amount of elasticity.

If we accept Grünhagen's assertions that no *m. dilator pupillæ*

---

[1] *Archiv f. mikroscop. Anat.* Bd. 25, s. 1.

exists, it follows that the nerves which dilate the pupil must act upon the sphincter muscle : in other words, these nerves are the inhibitory or dilator nerves of that muscle[1].

The experiments of Grünhagen afford strong proof of the presence in the sphincter muscle of nerve fibres which relax that muscle. He has shown that the suspended sphincter can be made to elongate by direct stimulation of the muscle itself. An inhibitory effect can therefore be produced upon this muscle by the direct action of a stimulus in precisely the same way as I have shown to take place in the auricular muscle of the heart of the frog, tortoise or crocodile, and in the ventricular muscle of the frog, when a strip of that muscle is suspended and a weak inter-rupted current is sent through that strip. In this latter case I have come to the conclusion that the inhibitory effect of the direct stimulus to the cardiac muscle is due to the stimulation of inhibitory nerve fibres in the muscle strip. It is therefore highly probable that the relaxation of the suspended sphincter muscle which occurs upon direct stimulation is also due to the action of inhibitory nerves in that muscle.

Finally, it is a striking and highly suggestive fact that the anatomical course and histological characters of the nerves which dilate the pupil are precisely similar to the inhibitory nerves of the circular muscles of the intestine, &c. which run in the abdominal splanchnic nerves. In both cases they leave the central nervous system in the thoracic outflow of visceral nerves, the one passing out in those upper *rami viscerales* which are directed upwards to form the cervical splanchnic nerve, the other in those lower *rami viscerales* which pass downwards to form the abdominal splanchnic nerves. In both cases they leave the central nervous system among the fine medullated fibres of the anterior roots, the special anterior roots which contain the dilators of the pupil being, according to Budge, 2nd, 3rd and 4th thoracic, according to my own observations in the dog more especially the 2nd thoracic; in the frog they pass out in the anterior root of the 4th nerve[2].

In both cases they pass over the lateral ganglia along the

---

[1] The only other theory of their action is the so-called hydraulic theory which supposes that the dilation of the pupil takes place by means of the contraction of the blood-vessels of the iris. In this case these dilator nerves would be vaso-constrictor nerves. This hypothesis is clearly not worthy of serious consideration, and is at once overthrown by the fact that these nerves can cause most marked dilation of the pupil an hour or more after the death of the animal when the circulation has absolutely ceased.

[2] Ferrier and Yeo (*Proc. Roy. Soc.* 1881, Vol. xxxii., p. 17) noticed that in th monkey stimulation of the anterior roots from the 1st thoracic up to the 4th cervical caused no alteration in the size of the pupil.

corresponding splanchnic nerves to the distal ganglia before they alter their character; the one passing directly to the superior cervical ganglion in the bundle of fine medullated fibres which can be dissected out of the conjoint vago-sympathetic nerve in the neck; the other in the bundle of similar fibres which passes along the abdominal splanchnics into the semilunar ganglia. In both cases they cannot be traced further as medullated fibres; in the one case they in all probability lose their medulla in the distal semilunar ganglia, in the other, with equal probability, in the distal superior cervical ganglion.

The histological, anatomical and physiological evidence then all point to the same conclusion, viz., that in the sphincter muscle of the iris we have yet another example of a muscular structure supplied by two nerves of opposite character, the one motor and the other inhibitory.

Further the conclusion is forced upon us that, in those animals which are unprovided with any special radial muscular fibres, the dilation of the pupil which occurs upon stimulation of the dilator nerves is brought about solely by the inhibition of the tonic contraction of the sphincter muscle in conjunction with the elasticity of the posterior limiting membrane or other parts of the iris, in consequence of which the pupillary edge of the iris naturally falls back when the sphincter muscle is relaxed.

Chapter II. On the nature of the action of the motor and inhibitory nerves of the vascular and visceral muscles.

The evidence which has been given in the preceding pages is sufficient to show that the inhibitory nerves are of as fundamental importance in the economy of the body as the motor nerves. No evidence exists that the same nerve fibre is sometimes capable of acting as a motor nerve, sometimes as a nerve of inhibition, but on the contrary the latter nerves form a separate and complete nervous system subject to as definite anatomical and histological laws as the former; the complete investigation of these laws is one of the most important problems of physiology, and is absolutely necessary before we can attempt to understand the part played by the nervous system in the regulation of the different vital processes.

From what has been said we may with safety draw the conclusion that the muscular tissue of both the visceral and vascular systems is supplied by two sets of nerves, of which the one sets that tissue in

activity and causes contraction, the other inhibits its action and causes relaxation; further, no explanation of the action of this latter set of nerves can be satisfactory which is not as far reaching and fundamental in its character as that given for the action of the former set.

I propose then in this chapter to give such an explanation of the opposite actions of these two sets of nerves as shall place the nerves of inhibition upon an equal footing with motor nerves. My arguments are necessarily based entirely upon the action of the cardiac nerves, for in their case only have we sufficient data on which to build a theory. But the structural and anatomical affinities of these nerves to other corresponding nerves of the vascular and visceral systems have been so clearly proved in the foregoing pages that it is allowable to assume that any theory of their action must of necessity apply to those other nerves as well.

SECTION I. *On the nature of the action of sympathetic cardiac nerves.*

So long as the accelerator nerves were known to exist only in warm-blooded animals it was difficult to obtain sufficiently reliable data upon which to found a theory of their action. Since, however, I have been able to show that these nerves exist equally in various cold-blooded animals, such as the crocodile, frog and tortoise[1], it has been possible to enlarge our knowledge of their action very considerably, and I propose therefore in the first place to show that such nerves belong functionally as well as structurally and anatomically to the group of vaso-motor nerves.

In the spring of 1881[2], a full year before the publication of Heidenhain's paper[3], I published a preliminary account of various experiments upon the action of the vagus nerve on the heart of the frog, which showed that this nerve was capable not only of accelerating the heart's action but also of greatly increasing the strength of its contractions. A fuller report of these experiments was given at the London meeting of the International Medical Congress and the full paper was read before the Royal Society in December of that year. In this paper I was under the delusion that the frog's heart was supplied with only one nerve, viz. the vagus, and therefore attributed both the acceleration and augmentation observed to the action of the fibres of that nerve.

[1] *Op. cit.*
[2] *Proc. Camb. Phil. Soc.*, March 7, 1881. Vol. IV., p. 75.
[3] *Pflüger's Archiv.* Bd. XXVII. s. 383.

The subsequent discovery that the vagus of the frog was in reality the vago-sympathetic nerve enabled me for the first time to dissociate the action of these two nerves upon the heart of that animal, and therefore to study the effect of the sympathetic cardiac nerves free from admixture with the vagus fibres. The tracings so obtained showed clearly that the primary effect of the stimulation of the sympathetic is a marked increase both in the rate and strength of the contractions of both auricle and ventricle.

Similar results were obtained both from the tortoise and the crocodile, with the exception that the action of these fibres is in these animals almost if not entirely confined to the contractions of the auricle.

I can then assert positively that the action of the sympathetic cardiac nerves is to cause an increase in the strength as well as in the rate of the contractions of the cardiac muscle. In so far therefore as a nerve is motor, because it increases the activity of an already active muscle, these nerves can be called motor nerves.

A motor nerve also sets in action a muscle when it is at rest. This is so far true of these cardiac nerves in that they are able to set the heart beating vigorously and regularly when it is apparently at rest. I have often kept the frog upon which I have been experimenting until the next morning and found its heart flaccid and apparently motionless, no trace of contraction of either auricles or ventricle was to be seen; upon then stimulating the sympathetic nerve, in a few seconds both auricles and ventricle began to beat, and soon the whole heart was contracting regularly and strongly. I have seen a similar result with both the crocodile and the tortoise. A closer examination showed that although the heart was to all appearance pulseless yet in reality the sinus was still contracting; in every case careful observation has enabled me to detect weak often slow yet regular sinus contractions which were not able to travel into the auricle and so to the ventricle. In one case where I could see no movement whatever of the sinus proper, I noticed the superior venæ cavæ still contracting rhythmically. Although therefore we can truly say that the sympathetic cardiac nerves can set in action the auricular and ventricular muscles when at rest, we cannot say that they can cause the heart as a whole to beat when it is motionless. The action of the nerve is perhaps rather to improve the conduction power of the different muscular tissues which together form the heart than to actually excite into action any part of those tissues. We know that in the heart left alone in the body the process of dying is characterized by the formation of successive blocks to the peristaltic

wave of contraction as it passes from one heart cavity to another; first the ventricle ceases to respond to the auricle, then the auricles do not answer to every sinus contraction, and finally it is possible to conceive that a block may ensue between the large veins and the sinus itself; at the junction then of each separate cavity with the next in order a marked tendency to the interruption of the regular sequence exists, so that the restoration of the contractions to auricles and to ventricle, and even to the sinus itself, which occurs when by stimulation of the sympathetic the apparently pulseless heart is made to beat again, denotes probably the power of the nerve in restoring the sequence of the contractions, i.e. according to the views expressed by me in a former paper[1], in increasing the conductivity of the cardiac muscle just as it increases the contracting power and the rate of rhythm of that muscle.

This action of the sympathetic, viz. the restoration of the sequence between the contractions of the auricles and ventricle of the frog's heart can be inferred from the results of my paper in the *Phil. Trans.* 1882, where as was noted at the time, and as may be seen in Figs. 17, 18, Pl. 69, the restoration of the sequence between auricle and ventricle due to the action of the vago-sympathetic nerve when a block had been caused by clamping or otherwise, is coincident with the period of maximum contractions, i.e. occurs when the action of the sympathetic is at its maximum. In many cases noticed in that paper, of which an example is given in Fig. 18, Pl. 69, this restoration of sequence took place upon vago-sympathetic stimulation when at the same time the curves showed that the inhibitory fibres of that nerve had not been set in action so that sympathetic effects were alone visible.

During 1884 I have repeated these same experiments a few times with the sympathetic alone and the intra-cranial vagus alone, and have obtained undoubted evidence that the sympathetic is able to restore the sequence between auricle and ventricle at the same time that it increases the force of the contractions.

I conclude therefore that the primary effect of these nerves is to increase the activity of the cardiac muscle in all directions; they increase the rhythmical power, the contraction power and the conduction power of the muscular tissues. In fact they act in all these respects just as we should expect a motor nerve to act if the muscle it supplied was not at rest but in an active condition.

[1] This Journ., Vol. iv. p. 43.

Our knowledge of the action of any nerve is not however complete as long as we only know its primary action; the chemical changes which the action of the nerve sets up in the tissue must manifest themselves in a more or less permanent after-effect which must be recognizable apart from the more temporary primary effect of the stimulation of the nerve. Thus we recognize that a motor nerve causes a muscular contraction by means of chemical changes in the muscle which are of a destructive nature, so that the after-effect upon the muscle is in the direction of exhaustion; and if the activity of the muscle be long continued this exhaustion becomes very manifest. In describing the phenomena accompanying the action of a motor nerve the subsequent exhaustion is as important a factor as the contraction of the muscle.

If therefore the sympathetic cardiac nerves are the motor nerves of a rhythmically active muscle, it follows that part of their action, and that by no means an unimportant part, must show itself as an after exhaustion. Now we know that the cardiac muscle when exhausted contracts like all other contractile tissues less strongly, and we also know that one of the most characteristic signs of exhaustion in the heart as a whole is the gradual failure of the regular sequence in the contractions of its different cavities. By these two characteristic signs the sympathetic manifests its relationship to motor nerves.

In my paper in the *Phil. Trans.* 1882 I noticed (see Fig. 9, Pl. 68), that the augmentation of the auricular contractions in the toad consequent upon vago-sympathetic stimulation was followed by a diminution in the size of those contractions with a subsequent return to the same height as before the stimulation of the nerve. In some of the curves then obtained it is seen that this after diminution took place when, as far as can be judged from the absence of any primary inhibitory effect, the sympathetic fibres were alone affected by the stimulation. This diminution of the strength of the auricular contractions puzzled me at the time, and I did not attempt to give any explanation of it. In the light however of further evidence, which I have been able to obtain since the date of the publication of that paper, it seems clear that such diminution expresses the amount of exhaustion in the auricular muscle due to the motor influence of the stimulated sympathetic nerve.

In order to determine this point I argued that if the sympathetic nerve was motor in its action, then the exhaustion which follows in consequence of each stimulation must be still more striking at the end of a series of long and powerful stimulations following each other at short intervals; I therefore compared the contractions of a number of hearts

whose sympathetic nerves had been strongly stimulated for a long period with others in which either the cardiac nerves had not been stimulated at all or the intra-cranial vagus had been excited in the same manner as the sympathetic. In some cases the heart was suspended and tracings taken both of auricular and ventricular contractions; in others the comparison was made by direct observation of the hearts *in situ*, the frogs being placed side by side.

Such experiments show that the rapidity with which the force of the contractions diminishes during the course of each experiment is decidedly accelerated by strong stimulation of the sympathetic nerve, the contractions becoming weaker after such a stimulation than they would have been if the intra-cranial vagus had been stimulated or even if the heart nerves had been left at rest.

In the same set of experiments I was able to observe the exhausting after-effects of sympathetic stimulation upon the sequence of the ventricular and auricular contractions. I have noticed again and again in the case of the suspended heart with the clamp in the auriculo-ventricular groove that a comparatively slight increase in the tightness of the clamp is sufficient to prevent the contractions from passing into the ventricle, provided that the sympathetic nerve had been previously stimulated for some time; on the other hand, it is wonderful how tightly that clamp must be screwed together before a block is caused after a series of stimulations of the intra-cranial vagus.

Further without altering the position of the clamp, when the ventricle is responding with perfect regularity to every auricular contraction, the exhaustive after-effect of the stimulation of the sympathetic is manifested by the frequent omission of ventricular contractions. The failure of sequence so caused is as a rule irregular in its character, so that the ventricle fails every now and then to respond to an auricular contraction instead of failing regularly after every second or third contraction of the auricles.

From these observations it follows that the cardiac sympathetic nerves belong to the group of motor vascular nerves because they augment the activity of the cardiac muscle, and that augmentation is followed by exhaustion. We may therefore call them the motor nerves of the heart and class them functionally as well as structurally and anatomically with the other motor vascular nerves. Seeing however that nerves of the same character exist in all probability for all organs and tissues of the body, whether they are muscular or not, it is better to use some other term than motor in speaking of such nerves, some term

which shall be of wider application and yet shall denote their main characteristics.

When a tissue such as a muscle is said to be at rest we know that in reality a continual interchange of material or metabolism is all the time taking place, the condition of equilibrium which we denote by the term rest being brought about by the counterbalancing of the two opposite processes of destructive and constructive metabolism, or as Hering has called them of assimilation and dissimilation. In other words metabolism includes the two opposite processes of destruction and construction, or as they may be called of katabolism and anabolism. When the muscle is set in activity by stimulation of its motor nerve or otherwise then a great increase in the destructive changes occurs with subsequent exhaustion until by gradual repair the former condition of the tissue is restored. We can therefore with justice speak of the motor nerve of a muscle as the katabolic nerve of that tissue; and seeing that such a term is applicable to the destructive metabolism of all tissues whether contractile or not it is better to speak of the sympathetic cardiac nerves as the katabolic rather than the motor nerves of the heart.

SECTION II. *On the nature of the action of the cardiac vagus nerves.*

Last year at the International Medical Congress at Copenhagen I read a paper on Inhibition, in which I gave my reasons for considering the inhibitory cardiac nerves as nerves which brought about a constructive and not a destructive metabolism of the muscular tissue of the heart, as nerves therefore which may be called anabolic in contradistinction to the katabolic sympathetic nerves.

In that paper, which has just appeared, I discussed three questions; 1. Do the cardiac inhibitory nerves possess a separate existence? 2. Do they retain their inhibitory power right up to their termination in the cardiac muscular tissue? 3. Is the nature of their action upon the muscle constructive, destructive, or neutral?

The first question is answered in the affirmative by the fact that in all animals examined, inclusive of the frog, the accelerator and inhibitory fibres run a separate course, as already mentioned in previous sections of this paper.

The answer to the second question depends largely upon the interpretation of the inhibitory phenomena observed in any portion of the cardiac muscle upon direct stimulation of that portion. In a former

paper[1] I have shown that a diminution of the strength of the spontaneous or artificial rhythmical contractions of a strip of auricular muscle takes place when an interrupted current, too weak to cause contractions, is sent through that strip; and I pointed out that the explanation of the localized inhibition must be sought for either in the stimulation of inhibitory nerve fibres in that strip or else in the direct action of the interrupted current upon the muscular tissue. At that time I was inclined to accept the latter explanation without however being strongly persuaded one way or the other. Since that time further consideration and examination of this problem have led me definitely to the conclusion that the first explanation is the correct one, and that therefore the diminution of the contractions of the isolated muscular strip when a weak interrupted current passes through it is evidence of the existence of inhibitory nerve fibres in that strip; consequently the inhibitory nerves pass as such into the muscular tissue itself and act upon that tissue directly without the medium of any intermediate apparatus. The grounds for this conclusion are as follows:

In the first place, as originally pointed out, the weak interrupted current causes a diminution of the contractions of those muscular strips only which are taken from that part of the heart in which stimulation of the vagus causes a diminution of contraction, e.g. in muscle taken from both auricle and ventricle of the frog but from the auricle only of the tortoise.

Also atropin removes this action just as it prevents the effect of the vagus.

Both these facts show the close relationship between this action of direct stimulation and that of the vagus nerve.

Now in all these experiments the interrupted current was sent through the whole of the strip of suspended muscle while the single induction shocks were sent in at one end. Since that time I have varied the position of the two electrodes and have found that the same diminution of contractions takes place when the single induction shocks are sent through the whole strip and the interrupted current applied at one end, or when the two pairs of electrodes are applied to opposite ends of the strip. Moreover if the strip be held firmly in the middle by a clamp, and the single induction shocks be applied to the lower portion while the weak interrupted current is applied to the upper portion of the strip, then it is possible to clamp so tight that only the contractions

[1] This Journ., Vol. iv. p. 43.

of the lower portion of the strip are registered by the lever attached to the lower extremity, and yet to obtain a diminution of these contractions during the passage of the interrupted current through the upper half of the strip; in fact, the upper portion can be treated as a nerve supplying the lower. When the clamp is tightened sufficiently, then the stimulation of the upper portion is no longer able to produce any alteration in the strength of the contractions of the lower half, showing that the effect produced is not due to any escape of current on to the lower portion, for the continuity of the tissue still remains after the clamp had been tightened. These experiments show that such inhibition is not due to the direct action of the stimulus on the muscle but rather to the excitation of nerve fibres in the strip.

This conclusion receives confirmation also from the results of stimulation of the cardiac muscle after degeneration of the vagus nerve. In its behaviour to vagus stimulation the heart of the crocodile is very similar to that of the tortoise; the contractions of the auricles are chiefly influenced by the nerve and a strip of muscle taken from them responds to a weak interrupted current in precisely the same way as already noticed in the case of the tortoise. The diminution which a weak interrupted current sent through the strip produces in the contractions excited by single induction shocks is most marked. If however both vagi nerves have been cut some time before so that the cardiac fibres have degenerated, then it is extremely difficult to obtain any diminution of these contractions by the passage of the interrupted current. In some cases a very slight diminution was noticed, in others no effect whatever could be seen. With the degeneration of the inhibitory fibres the inhibitory power of a stimulus applied to the muscle directly more or less completely disappears, showing that such inhibition is in reality due to the stimulation of nerve fibres in the muscle itself.

Finally Ransom[1] has shown that the inhibitory effects produced by direct stimulation of the cardiac muscle of Invertebrata are also due to the action of inhibitory nerves in that muscle.

I consider it therefore as certain that the inhibitory nerves possess an independent existence, and that their function remains unaltered from their origin to their termination in the muscular tissues of the heart.

We come then now to the third question discussed at the Congress, viz. the nature of their action. I argued that the alteration in the

---

[1] This Journ., Vol. v. p. 261.

properties of the cardiac muscle caused by vagus stimulation must be brought about in one of three ways: the action of the nerve must be either neutral, destructive or constructive in its relations to the muscular tissue. The general view hitherto held has been that inhibition is to be explained by some process of interference which takes place in the nervous apparatus of the heart, and therefore the muscular tissue is only a passive instrument in the hands of such mechanism. Such an explanation is obviously untenable in the face of the evidence which now exists to show that all the properties of the muscular tissue are deeply affected by the stimulation of the inhibitory fibres, and that those fibres produce the same effects up to their termination in the muscular substance. Any explanation of inhibition which is to hold good must not confine itself merely to the cessation of rhythmical action, but must also explain the diminished contractions and the relaxation of the cardiac muscle.

It is perfectly possible to imagine that the depression of function which is the symptom of inhibitory action, the slowing of the rhythm, the diminution of the contractions, the relaxation of the muscle, the lowering of excitability and conductivity are all signs of some change in the properties of the muscular tissues akin to exhaustion; so that we might be tempted to describe the inhibitory phenomena as significant of destructive changes produced in the muscle by the action of the nerve. But exhaustion as we ordinarily know it is an after-effect of activity, whereas the phenomena we are now dealing with appear as the primary effect, and moreover are followed by results the very opposite of those of exhaustion. In the various papers[1] which I have written on the subject

[1] An apparent exception to this statement is found in the description of a demonstration of the action of the intra-cranial vagus nerve of the frog given before the members of the Physiological Society at Oxford. (Proc. Physiol. Soc., June 7, 1884. This Journ., Vol. v.) The description there given applied simply to the demonstration in question, and truly described what was seen at the time. I made use however of terms which were certainly not warranted by that demonstration; thus I spoke of a "permanent" weakening and of the production in the heart of "a condition very near to that of death" as the result of a series of intra-cranial vagus stimulations. This weakening of the heart's action is by no means permanent; it is true that after a series of stimulations of the intra-cranial vagus the slowing and weakening effect of the nerve stimulation may continue some time after the end of the last stimulation, but sooner or later the heart recovers and beats better and stronger than before, even without stimulation of the sympathetic nerve; there is no question whatever of a condition near to that of death. In the demonstration at Oxford I did not allow sufficient time after the last stimulation of the intra-cranial vagus nerve for this spontaneous recovery to take place, as I wanted to demonstrate the effect of stimulation of the sympathetic nerve upon the heart when it was beating weakly in consequence of vagus stimulation.

I have throughout shown that the inhibitory process is not harmful to the functions of the cardiac muscle, but that on the contrary the after-effect is a beneficial one; the rate of rhythm is maintained if the heart is beating at its normal rate, or it may be increased if it is beating abnormally slow, the contraction power is maintained or increased if exceptionally weak, the conduction power is regained, the damaged tissue is repaired as the ultimate consequence of stimulation of inhibitory fibres. In fact the result of stimulation of these nerves is exactly opposite to that of the sympathetic nerves; there, increased activity followed by exhaustion, symptoms of *kata-bolic* action: here, diminished activity followed by repair of function, symptoms of *anabolic* action.

There is then to my mind no greater mystery involved in the conception of a nerve of inhibition than in the conception of a nerve of a contraction. In the former case the cessation of function, the relaxation of tissue, is a symptom of constructive chemical changes going on in the tissue, i.e. of anabolism or assimilation or trophic action, in precisely the same way as the activity of function, the contraction of the tissue, is a symptom of destructive changes, i.e. of katabolism or dissimilation.

The nerves of the heart are the most perfect types of such opposite nerve actions, and to their further study I look with confidence for still more decisive proofs of this theory of inhibitory action; they do not however stand alone. The laws governing the structure and course of similar fibres throughout the body have been already indicated in these pages; the evidence is becoming daily stronger that every tissue is innervated by two sets of nerve fibres of opposite characters so that I look forward ·hopefully to the time when the whole nervous system shall be mapped out into two great districts of which the function of the one is katabolic, of the other anabolic, to the peripheral tissues : two great divisions of the nervous system which are occupied with chemical changes of a synthetical and analytical character respectively, which therefore in their action must show the characteristic signs of such opposite chemical processes.

At present our knowledge of such physical and chemical signs is confined almost entirely to those which are associated with katabolism and with the action of katabolic nerves. One of the chief physiological problems of the future is to establish the symptoms of anabolism in the same manner as has been done for its opponent; already we find the commencement of the performance of this task. The work done by Hering and Biedermann points directly to a separation of the two

processes of assimilation and dissimilation; and in a recent paper Biedermann[1] has shown that the inhibitory action of the constant current upon the veratrinized muscle of the frog is associated with a positive and not with a negative variation of the electrical current. Again quite recently Bayliss and Bradford[2] have demonstrated that the action of the chorda tympani on the submaxillary gland is associated with a positive variation of the electrical current while sympathetic stimulation causes a negative variation. If therefore other evidence tends to show that the former nerve contains fibres which are anabolic, while the latter nerves are katabolic to the gland tissue, this investigation appears to me to afford strong confirmation of such difference of action in these two nerves.

At present we possess indications only of such other evidence, yet such indications are distinctly in favour of the hypothesis here laid down. Judging from what has been already said upon the structure and distribution of the two nerves which supply the various salivary glands, we should rather expect to find the katabolic nerves in the so-called sympathetic supply and the anabolic in the so-called cerebro-spinal. Now Heidenhain has separated these nerves into two sets, the trophic and secretory nerves of the glands, these two sets corresponding very largely with the anatomical distribution; the sympathetic fibres are essentially trophic fibres, the cranial secretory. He makes use of the term "trophic" in a somewhat peculiar sense, not meaning thereby necessarily constructive changes in the gland substance, but simply changes which lead to the formation of the essential constituents of the gland secretion from the protoplasm of the gland. Such changes however are according to our present knowledge with much more probability brought about by the katabolism rather than by the anabolism of the protoplasmic meshwork; it would be better therefore to call such nerves "katabolic" rather than "trophic." The formation of granules upon stimulation of the sympathetic nerves takes place at the expense of the protoplasm of the gland cell.

On the other hand stimulation of the secretory nerves appears to produce a double effect. In a recent paper Langley[3] has brought forward evidence pointing strongly to the conclusion that the growth of the protoplasm in the gland cell is not brought about by the action of the so-called "trophic" nerves, but rather is under the control of the

[1] *Sitzb. d. Kaiserl. Akad. d. Wissensch.* 1885. III. Abtheil.
[2] "Proceedings of Physiol. Soc. 1885," p. xiii. in this Journ., Vol. VI.
[3] This Journ., Vol. VI. p. 89.

so-called "secretory" nerves; that therefore two sets of fibres must be distinguished in these latter nerves, the one secretory, by the action of which the water and granules are discharged from the cell, the other anabolic and concerned in the building up of the protoplasmic network.

These anabolic glandular nerves would then correspond anatomically as well as physiologically to the inhibitory nerves of muscular structures.

The decisive proof that inhibition is a symptom of anabolism in the same way as contraction is a symptom of katabolism will in all probability be found in the heart; and perhaps the most important investigation which must be done before this theory of anabolic nerves is based on an absolutely firm footing is to find out, what are the electrical and thermal changes in the heart muscle which accompany the stimulation of its inhibitory nerve fibres.

Finally, although in this paper I have carefully abstained from dealing with the structure and function of the afferent nerves, I desire to point out that this explanation of inhibition is applicable to inhibition occurring in the central nervous system as well as in peripheral tissues. We can speak of nerves which are excitor and inhibitory to the activity of nerve centres, as the katabolic and anabolic nerves of such centres, in the same way as we have used these terms for the corresponding peripheral nerves; and we can explain inhibition occurring through the action of an afferent nerve in one of two ways, either such nerve sets in action reflexly the anabolic nerve of the tissue, the activity of which is inhibited, or else it is itself the anabolic nerve of the centre which governs the activity of that tissue. As I hope to deal with the whole question of the structure, distribution and function of the afferent nerves in a subsequent paper it is not advisable to say more about the function of such nerves here.

PART II. ON SOME MORPHOLOGICAL POINTS CONNECTED WITH THE DISTRIBUTION OF THE VISCERAL AND VASCULAR NERVES.

SECTION I. *On the Morphology of the Superior Cervical Ganglion.*

I have already pointed out that the superior cervical ganglion must be looked upon as a distal ganglion, its only connection with the central nervous system being by means of the cervical splanchnic nerve. Such a conclusion is borne out by the investigation of this ganglion in various groups of animals.

The characteristic of this ganglion in mammals is its separate position from the neighbouring ganglia of the vagus and glossopharyngeal nerves, and its definite connection with the cervical splanchnic (cervical sympathetic), the nerves of which run right into it.

Another characteristic of mammals which coincides with the large size of the superior cervical ganglion, is the great development of the prevertebral or collateral ganglia in the abdominal region.

Among the Reptilia we find two types of arrangement in the cervical portion of the sympathetic system; one, as in crocodiles, which follows the avian type and consists of the regular continuation of the metameric lateral chain in the canalis vertebralis formed between the capitulum and tuberculum of the cervical ribs, with a cervical collateral chain in the shape of the *symp. impar*; the other, as in the tortoise, lizard, &c. which is formed on the mammalian type and consists of a superficial sympathetic nerve trunk passing upwards in the neck alongside of the vagus nerve and starting from the uppermost of those ganglia which lie close against the vertebræ. In addition to this nerve which is commonly called the superficial cervical sympathetic, a deep cervical sympathetic is usually described, which is free from ganglia and corresponds in part at all events to the plexus vertebralis of mammalia. In these latter cases only, i.e. in reptiles which do not possess complete cervical ribs, can we compare the arrangement of the cervical sympathetic nerve and its ganglia with that in mammals.

We find in Stannius the assertion that a *ganglion cervicale supremum* and a *ganglion cervicale medium* are frequently found in connection with the superficial cervical nerve in various classes of reptiles. Thus, (*Handbuch der Zootomie*, Siebold and Stannius, Bd. II. Wirbelthiere, S. 151) in the description of *Amphibia monopnoa :*—" Der Stamm des N. Vagus besitzt fast allgemein bei seinem Eintritt in die Brusthöhle eine Anschwellung (ganglion trunci) welche als Vereinigungspunkt in der Bahn des N. Vagus verlaufender sympathischer Elemente mit solchen, die aus den letzten Halsnerven stammen und als Ausgangspunkt von R. R. cardiaci, ein Ganglion cervicale medium vertritt."

Among the peculiarities of the *Sauria* they describe, p. 154, talking of the deep and superficial cervical sympathetic nerves " Beide pflegen mit dem, dem N. glossopharyngeus anliegenden, Ganglion cervicale supremum unmittelbar oder mittelbar verbunden zu sein."

In *Ophidia*, p. 156 :—" Was den N. sympathicus der Ophidia anbetrifft so ist das dem N. glossopharyngeus anliegende Ganglion cervicale supremum Sammelpunkt von Verbindungsschlingen der Hirnnerven."

In *Chelonia,* p. 157 :—" Eine Schlinge verbindet den N. facialis mit dem dem N. glossopharyngeus anliegenden Ganglion cervicale supremum. Von diesem aus ist der Grenzstrang zum N. vagus und hypoglossus erstreckt und dann als oberflächlicher Halsstamm neben dem N. vagus und dem Truncus caroticus verlaufend fortgesetzt. Er geht am Eingange der Brusthöhle über in ein Ganglion cervicale medium, das dem N. Vagus mehr oder minder dicht anliegt, mit ihm in Verbindung steht und dann bei manchen Chelonien ein ganglion trunci bildet."

From these descriptions alone it is nearly certain that the ganglion cervicale supremum of Stannius is in reality the ganglion petrosum of the glosso-pharyngeal, as most undoubtedly his ganglion cervicale medium is the ganglion trunci of the vagus nerve.

Fischer[1] was strongly persuaded of the identity of this ganglion with the ganglion petrosum as is seen in the following passage.

" Der Sammelpunkt des doppelten Kopftheils ist, wie vorhin dargethan, meistens ein in der Bahn des Glossopharyngeus gelegenes Ganglion, von uns nach Bendz' Vorgange als *ganglion petrosum* bezeichnet,—diese Anschwellung ist zugleich meist der Punkt, von wo aus der (oberflächliche) Halstheil des Sympathicus beginnt. Aus dieser Einmündung und Ausstrahlung sympathischer Fasern scheint zu folgen, dass das Ganglion selbst ein Knotenpunkt im System der sympathischen Schlingen sei, und etwa als *Ganglion cervicale supremum* aufgefasst werden müsse. Müller ist (für *Python*) in der That dieser Ansicht. Da indessen das Ganglion cervicale supremum eine Anschwellung ist, die im Grenzstrange selbst liegt, und von dem aus Manche den Kopftheil des Sympathicus nach vorn (oben), den Halstheil nach hinten (unten) ausstrahlen lassen, so widersteht der Deutung unseres Ganglions als Ganglion cervicale supremum der Umstand, dass nicht immer die Kopftheile des Sympathicus in dasselbe einmünden, sondern zuweilen diese Anschwellung umgehend, und nur durch feine Verbindungszweige oder gar nicht mit ihm verknüpft, sich direct in den Halstheil des Sympathicus fortsetzen. Da hingegen dies Ganglion, wo es auch sei, immer in der Bahn des Glossopharyngeus liegt, so scheint die Bezeichnung desselben als Ganglion petrosum die einzig richtige zu sein."

As far as I myself have examined the question there can be no doubt of its identity. In the first place it is impossible of belief that a large sympathetic ganglion should be found in the snakes in this one position when no other ganglia of either the lateral or collateral

[1] *Op. cit.* p. 196.

systems are known to exist in these animals. In the second place an examination of freshly-killed specimens of *Testudo Græca* and *Lacerta ocellata* gives the clearest evidence that the cervical sympathetic does not pass into this ganglion on the glosso-pharyngeal but only passes by it or over it, sending branches to the ganglion but never entering into it, as would be the case if it truly corresponded to the superior cervical ganglion of Mammalia. (See figures in Fischer.)

I have examined this question with especial care in the tortoise (*Testudo Græca*) for Martin and Moale[1] in their description of an allied species *Pseudemys rugosa* describe a superior cervical ganglion with which both vagus and glosso-pharyngeal are in connection.

At first sight the cervical sympathetic of the tortoise appears undoubtedly to enter into the lowermost of the two upper ganglia of the vagus, and without closer examination it is very natural to call this second ganglion the superior cervical; for in the vagus of this animal we find three distinct ganglia, the uppermost of which would therefore be the ganglion jugulare, the second the superior cervical, and the third, which is situated low down at the commencement of the thoracic portion of the nerve, the ganglion trunci. An examination however of either a fresh or an osmic preparation under a dissecting lens shows that the cervical sympathetic simply lies against the ganglion and does not enter into it; with a pair of needles it can be isolated as a separate nerve just as easily in its passage under the ganglion as in its course alongside the main trunk of the vagus nerve. The relation of this second ganglion on the vagus of this animal to the ganglion petrosum of the glosso-pharyngeal will be dealt with subsequently.

The evidence then strongly points to the conclusion that in those cold-blooded animals which possess a cervical sympathetic of the same nature as that found in mammalia no superior cervical ganglion exists; and correlated with the absence of this ganglion we find that the collateral ganglia are inconspicuous or absent although at the same time the lateral ganglia are well formed and conspicuous. From morphological considerations therefore it would appear that this ganglion belongs rather to the collateral than to the lateral group of ganglia. The evidence of morphology is in harmony with that of anatomy and physiology and confirms the view put forward in the preceding pages that the superior cervical ganglion belongs to the distal rather than to the proximal group of ganglia.

[1] *How to dissect a Chelonian.* New York, 1881.

SECT. II.   *On the central origin of the ramus visceralis.*

The evidence which has already been given shows that the rami
viscerales do not arise equally from all parts of the central nervous
system, but from certain limited portions of it, viz. from three regions,
the limits of which I have given under the title of cervico-cranial,
thoracic and sacral regions.   It is possible to go further than this and
to trace them to their origin in the central nervous system.   The
central grey matter of the spinal cord contains nerve cells which are
divisible into four groups, those of the anterior and posterior horns,
and those of the lateral horn and of Clarke's column.   Now we find
that the two first of these groups of cells form continuous columns
along the whole length of the spinal cord; and that the lateral group
forms a distinct column in all parts except the cervical and lumbar
swellings, where it is undistinguishable from the cells of the anterior
horn.   Clarke's column or the columna vesicularis on the other hand
forms a discontinuous column, the cell groups of which it is composed
being very definitely limited to certain regions.   These regions are
divisible into (1) a cervico-cranial region, (2) a thoracic region, and (3) a
sacral region.

This column of cells is most conspicuous in the thoracic region; it
commences at the origin of the 2nd thoracic nerve and continues along
the whole thoracic part of the cord to about the origin of the 2nd
lumbar nerves; corresponding therefore absolutely to the region of the
thoracic outflow of visceral nerves.   Below the level of the 2nd lumbar
nerve a localized nucleus of cells belonging to this cell column is known
in the sacral region as "Stilling's sacral nucleus," corresponding
closely in position to the sacral outflow of visceral nerves.   Above the
level of the 2nd thoracic nerve this column of cells again makes its
appearance at the level of the 2nd cervical nerve, forming the so-called
cervical nucleus.   Above this point its continuation leads into part of
the nuclei of the vagus and glosso-pharyngeal nerves.

This appearance of the nerve cells of Clarke's column in the cervical
region coincides with the appearance of the bundles of very fine
medullated fibres in the spinal accessory nerve, and the continuation
upwards of the column into the nuclei of the lower cranial nerves
coincides with the cervico-cranial outflow of visceral nerves as a
whole.

Although as yet the fine medullated fibres which constitute the

rami viscerales have not been directly traced into the cells of the columnæ vesiculares, the connection of these fibres with this column of cells is to my mind proved conclusively by the fact that the cells of Clarke's column are confined to those regions of the central nervous system which give origin to the rami viscerales.

It by no means follows that the origin of the ramus visceralis is settled because it can be proved to arise from Clarke's column. It possesses in addition certain important relations with the cells of the lateral horn. These relations can be best explained by the description of the formation and meaning of the rami viscerales of the upper cervical region.

In this region we find that each segment gives origin not to two roots only, as in the thoracic and lumbar regions, but to three, viz. anterior, posterior, and lateral roots. The anterior and posterior roots unite to form the 1st, 2nd, etc. cervical nerves, while the lateral roots unite to form the spinal accessory. The spinal accessory in fact is formed by certain distinct elements belonging to a number of spinal nerves, which elements may be spoken of as forming a lateral group of nerve roots distinct from the anterior and posterior groups.

When we examine the composition of this nerve which is derived exclusively from lateral roots we find, as already mentioned (p. 10, cf. Fig. 7, Pl. IV.), that it is composed of two distinct portions, the one (A, in the figure) containing large medullated fibres, and the other (V) very fine medullated fibres with a few large ones interspersed. These two portions form a single nerve enclosed in its connective tissue sheath; when however this nerve has passed the ganglion jugulare vagi it separates into two branches, of which the one, the external branch, is non-ganglionated and supplies the trapezius and sterno-cleido-mastoid muscles; the other, the internal branch, is ganglionated and is lost in the ganglion trunci vagi. These two branches of the nerve correspond respectively to the two portions A and V of the above-mentioned figure.

We may therefore speak of this nerve as composed of two roots, a ganglionated and a non-ganglionated root. The ganglionated root has been already shown to have connection with the cells of Clarke's column; and the non-ganglionated, i.e. the motor fibres of the trapezius and sterno-cleido-mastoid muscles, are known to arise from the cells of the lateral horn. It follows that the lateral roots of this region are distinguished from the anterior and posterior roots not only by their

separate course outside the spinal cord but by their origin from separate centres in the cord itself.

Further, seeing that these special cell groups, viz. the cells of the lateral horn and of Clarke's column, are not confined to this special portion of the spinal cord but occur in other regions and indeed must be regarded as forming important parts of the structure of each perfect spinal metamere, it follows that the spinal accessory must not be regarded as composed of nerve fibres, the homologues of which do not exist in the anterior and posterior roots of the thoracic and lumbo-sacral regions; but that, on the contrary, we must look upon every spinal nerve as made up of three roots, one of which, viz. the lateral root, is mixed up with the other two in all regions of the spinal cord below the cervical, although still retaining its separate centres of origin.

If therefore we consider the nerve roots which arise from the upper cervical segments as typical of the formation of all spinal nerve roots, we may speak of the nerves which arise from each spinal segment as formed by three roots,

1. An anterior non-ganglionated root in connection with the cells of the anterior horn.

2. A posterior ganglionated root in connection with the cells of the posterior horn.

3. A lateral root, which is again divisible into

a. A ganglionated root in connection with the cells of Clarke's column.

b. A non-ganglionated root in connection with the cells of the lateral horn.

From this description it is clear that the triple arrangement of the nerve roots is formed by the combination of two symmetrical pairs of roots, each pair arising from a pair of nerve centres and composed of a ganglionated and non-ganglionated portion; in fact we may describe the nerve roots of each segment as composed of two roots, (1) an antero-posterior root and (2) a lateral root.

Now we know that one of the main characteristics of the posterior root is to supply cutaneous surfaces with afferent sensory nerves; while the characteristic of the non-ganglionated anterior root is to supply certain skeletal muscles with efferent motor nerves.

From these two general characteristics therefore we might use the term "somatic" in speaking of a nerve composed entirely of such anterior and posterior roots.

On the other hand we have seen that the evidence of the upper part

of the central axis shows that the lateral root gives origin to the ramus visceralis, as well as to motor nerves of certain skeletal muscles; this root might therefore be called "splanchnic" in contradistinction to the somatic root.

We could therefore describe each regular spinal nerve as arising by a somatic and splanchnic root. At present I use these terms chiefly for convenience of description, with the special object of emphasizing the distinction in the nerve supply of two distinct groups of skeletal muscles. The possible embryological reason for the existence of these two separate muscular groups will be briefly considered later on in this paper.

In accordance with this view I would describe the origin of the nerves of each spinal segment as follows.

Every segment gives origin to two roots, (1) a somatic root, (2) a splanchnic root.

The somatic root is composed of two portions, a ganglionated and a non-ganglionated portion, and arises from two columns of nerve cells, viz. the cell columns of the posterior and anterior horns respectively.

The splanchnic root is composed also of two portions, a ganglionated and a non-ganglionated portion, and arises also from two columns of nerve cells, viz. the column of Clarke and that of the lateral horn.

The non-ganglionated portion of the somatic root together with that of the splanchnic root supplies the skeletal muscular system with motor nerves. Such nerves undoubtedly arise from the cells of the anterior and lateral horns. I do not however think that we are justified in believing that the cell groups of the lateral horn are connected only with such motor nerves. The experiments upon the position of the vaso-motor centre conducted in Ludwig's laboratory seem to show that the vaso-motor nerves not only pass along the cord from the medulla oblongata in lateral tracts, but also are in close connection with a group of nerve cells in the medulla known as the antero-lateral nucleus of Clarke. This group of nerve cells is apparently an isolated portion of the cell column of the lateral horn which has been cut off by the crossing of the pyramids. It is therefore possible that the cell column of the lateral horn has a connection with vaso-motor nerves as well as with ordinary motor nerves. In this case we must look upon the ramus visceralis as arising not wholly from the cells of Clarke's column but also from those of the lateral horn.

It is impossible, with our present knowledge, to separate from each other the somatic and splanchnic roots in the lower regions of the spinal cord in the same manner as in the cervical region. I have however very little doubt that a more complete knowledge of the nerve supply of certain groups of muscles, especially of the muscles of respiraration, will enable us to define the splanchnic root with as much ease in these parts as in the upper cervical region. Already I have been able to notice some striking resemblances between the formation of certain rami viscerales and of the spinal accessory.

The external branch of the spinal accessory is not only motor to the trapezius and sterno-cleido-mastoid muscles, but also forms a communicating branch with the cervical plexus. Also, as has been already pointed out, no rami viscerales are formed in connection with either the cervical or brachial plexuses. We find the first ramus visceralis belonging to the thoracic outflow of visceral nerves in connection with the first nerve below the brachial plexus, i.e. the 10th spinal or 2nd thoracic; this nerve sends a small communicating branch to the 1st thoracic nerve, i.e. to the brachial plexus. It is to my mind a most significant fact that this communicating branch bears the same relation to the ramus visceralis that the external branch of the accessory nerve bears to its internal branch. The white ramus communicans of the 10th spinal nerve (2nd thoracic) is large and is composed of many separate bundles; the largest of these bundles arises directly from this small branch of communication with the brachial plexus, and not from the main part of the 10th nerve. In Fig. 6, Pl. IV., I give a section of this communicating branch after it has left the main stem of the 10th (2nd thoracic) nerve. As is seen, it is composed of two parts, the one, *A*, chiefly containing large medullated fibres; the other, *V*, chiefly containing very fine medullated; as we trace the series of sections further and further from the origin of the nerve, we find the two portions separate more and more from each other, and at last the nerve splits into an external and internal branch in precisely the same way as the spinal accessory; the external branch carries off the large medullated nonganglionated portion and forms the branch of communication with the brachial plexus, while the internal branch is composed of the fine medullated portion and passes to the ganglion stellatum as a ramus visceralis.

In fact the formation of this nerve is precisely similar to what I have described as a typical splanchnic root in the upper cervical region.

If we pass down to the lower limit of the thoracic outflow of visceral

nerves we find again the same formation; the rami viscerales of the 24th and 25th nerves (1st and 2nd lumbar) arise from those branches which form the genital branch of the genito-crural nerve rather than from the main stem of the 1st and 2nd lumbar nerves respectively.

This resemblance of structure affords the hope that subsequent investigation may enable us to map out those muscles which are supplied by the large motor fibres of the splanchnic roots; at the same time it points strongly to the conclusion that the ganglia of the sympathetic system are homologous to the ganglion trunci vagi and form the ganglia of the ganglionated portion of the splanchnic roots.

SECT. III. *On the relation of the posterior root ganglia to the visceral nerves.*

The ganglia of the main sympathetic chain must, according to Onodi[1], be considered as offshoots (Abkömmlinge) of the posterior root ganglia. If this is so, we may conceive that the posterior root ganglion in the thoracic region may be double, part belonging to the somatic, part to the splanchnic root. Remak described the origin of non-medullated fibres from the posterior root ganglion as well as from the sympathetic ganglia.

Undoubtedly grey non-medullated fibres are found in the white rami communicantes of the thoracic region; there is no evidence whatever that these non-medullated fibres arise from the anterior roots, while there is strong evidence that they arise from the posterior root ganglion.

The connection of the fibres of the ramus visceralis with the cells of the ganglion on the posterior roots of the thoracic nerves is most clearly visible in the case of the tortoise. In this animal the ramus visceralis does not spring from the ventral branch of the spinal nerve as in mammalia, but arises directly from the ganglion on the posterior root. In Fig. 1, Pl. IV., I give a representation of the connection between the sympathetic ganglia and the thoracic nerves from the 2nd to the 6th inclusive. As is seen, the ramus communicans directly connects each posterior root ganglion with its corresponding sympathetic ganglion. Owing to the insertion of the *lumbo-caudalis* muscle the rami communicantes of the 4th, 5th, 6th thoracic nerves at first pass out of the posterior root ganglion in the direction of the roots of the nerves, and then turn over

[1] *Op. cit.* p. 153.

the muscle to reach the sympathetic chain. In consequence of this arrangement, as is seen in Fig. 1, Pl. IV., a series of sections made for the purpose of following the spinal roots into the ganglion will at the same time enable us to trace the ramus communicans into the ganglion. In Figs. 2, 3, 4, 5, Pl. IV., I give drawings made from photographs of four sections taken from a consecutive series through the roots and spinal ganglion of the 4th thoracic nerve after staining with osmic acid. The figures show clearly how ganglion cells are formed in the ramus visceralis independently of those formed round the spinal roots, how these sympathetic ganglion cells increase in number as the posterior root ganglion is approached, and, finally, how they pass into and are lost in among the cells of the posterior root ganglion itself. Such a series makes it certain that in this case some of the nerve cells of the posterior root ganglion are connected with the fibres of the ramus visceralis.

Further, there is no reason to suppose that the arrangement of the nerves in the tortoise is fundamentally different from that of other vertebrates; I do not for instance mean to imply that the apparent origin of the whole ramus visceralis from the posterior root ganglion signifies that none of its fibres pass out from the central nervous system in anterior roots. As a matter of fact both anterior and posterior roots pass into the root ganglion in this portion of the spinal cord. Doubtless the large motor nerves of the anterior roots run through the ganglion and do not communicate with its nerve cells; at the same time they are so much lost among the mass of nerve cells that they cannot be followed as a separate bundle. It is therefore natural in this region for the visceral fibres of the anterior root to pass out from among the cells of the posterior root ganglion.

This amalgamation of posterior and anterior roots on the central side of the posterior root ganglion, so that both roots pass into the ganglion, is not so exceptional as at first sight it appears. To my surprise I have found that the anterior roots of the 1st and 2nd cervical nerves in the dog do not run free from the posterior root ganglion, but just as in the thoracic nerves of the tortoise amalgamate with the posterior roots before entering into the ganglion, and can only be traced through the ganglion by most careful observation of the size of their nerve fibres.

From what has been said it is clear that in speaking of the ganglia on the posterior roots we must always bear in mind the possibility that any such ganglion may belong both to the somatic and to the splanchnic root, or may belong entirely to the somatic or entirely to the

splanchnic. The appreciation of the possible double nature of this ganglion doubtless harmonizes the two apparently contradictory assertions of Onodi[1] on the one hand, and Beard[2] and Froriep[3] on the other; the former, as already stated, looked upon the sympathetic ganglia as offshoots of the posterior root ganglia; the latter observers have shown that the posterior root ganglion is developed in connection with certain cutaneous sense organs. The former was dealing with the ganglia of the splanchnic root, the latter with the ganglia of the somatic root.

The difference between the ganglia of the somatic and splanchnic roots would seem to consist in the fixed position of the former as compared with that of the latter. The ganglion of the somatic root always holds a definite position on the posterior root; the ganglion of the splanchnic root is no longer confined to any single position, its component parts are scattered among the various ganglia of the so-called sympathetic system, a small portion still remaining as part of the ganglion of the posterior root.

The way in which this scattering of the nerve cell-groups of the splanchnic root ganglion has arisen in opposition to the concentration of the cells of the somatic root ganglion will be made clear when morphologists have given us a trustworthy account of the phylogenetic development of the so-called sympathetic system. I look forward to the solution of this problem with the greatest interest as well as to the solution of the other perhaps still more important question, viz. what are the voluntary muscles which are supplied by the non-ganglionated portion of the splanchnic root?

An answer to this latter question has already been given by one of the greatest of English physiologists. Charles Bell, in his description of the nerves of the body[4], was the first to draw attention to the triple nature of the nerve roots throughout the central nervous system. He divided them into three sets: 1, anterior, containing the fibres of common voluntary motion; 2, posterior, containing the nerves of sensation; 3, lateral or respiratory, containing nerves which excite motions dependent on or related to the act of respiration. He says[5]

"I imagine that the same column or tract which gives origin to the fourth, seventh, glosso-pharyngeal, par vagum, and spinal accessory

[1] Loc. cit.
[2] Zoologische Anzeiger, April 20, 1885.
[3] Archiv f. Anat. u. Physiol. Anat. Abth. 1885, s. 1.
[4] The nervous system of the human body. London, 1830.
[5] Op. cit. p. 49.

nerves is continued downwards along the lateral parts of the spinal marrow, and that it affords roots to the spinal nerves, constituting them respiratory nerves as well as nerves of motion and sensation; and that it especially supplies the roots of the diaphragmatic nerve, and the external respiratory nerve."

Charles Bell himself was, I understand, more proud of this conception of special lateral or respiratory roots than of his famous functional separation of the anterior and posterior roots.

Physiologists have doubtless failed to follow up the clue thus given by Bell because the full bearing of this triple arrangement of the nerve roots was not immediately evident like the separation of anterior motor from posterior sensory roots. Now, however, we can see the importance of his conception; we see that this lateral tract of nerve roots, these so-called respiratory nerves, are the same as the non-ganglionated part of the splanchnic root. The significance of this agreement between Bell's conception and mine is apparent on the face of it; by respiratory nerves he meant, as he himself describes, those nerves which are dependent on or related to the act of respiration. The muscles in question included those of deglutition, of phonation, of smelling, &c., as well as the more purely respiratory muscles.

This conception of Bell's has, it appears to me, received the most important confirmation in a paper by Van Wijhe[1]. He points out firstly that the mesoblast plates are divided in the head into a double set of segments, viz. (1) a dorsal series, forming 9 separate "somites," and (2) a ventral series, forming a series of lateral plates (Seitenplatten).

The muscles which are formed from the somites (myotomes) are the muscles of the eye, supplied by the IIIrd, IVth, and VIth nerves, and those supplied by the hypoglossal nerve, i.e. muscles supplied by nerves which correspond to anterior roots.

On the other hand, all the muscles of the jaw and of mastication are derived from the segmental lateral plates, i.e. from the walls of the various visceral clefts (Visceralbogenhöhle). The nerves supplying the muscles formed from these lateral plates are clearly the same as Bell's cranial respiratory nerves (with the exception of the trochlearis) and form, according to my nomenclature, the non-ganglionated splanchnic roots of the cranial nerves.

If therefore Van Wijhe's separation of the skeletal muscles into two groups, of which the one is derived from the mesoblastic somites or

---

[1] "Ueber die Mesodermsegmente u. die Entwickl. der Nerven des Selachierkopfes." Amsterdam, 1882.

myotomes, and the other from the lateral plates of mesoblast, can be extended throughout the body, we find immediately a sufficient reason for the juxtaposition of the rami viscerales to the motor nerves of a special group of skeletal muscles. In accordance with this hypothesis I would define the non-ganglionated portion of the somatic root as supplying all the muscles of the somatic skeleton, i.e. muscles which are derived from the mesoblastic somites or myotomes; and the non-ganglionated portion of the splanchnic (lateral) root as supplying the muscles of the visceral skeleton, i.e. muscles which are derived from the lateral plates of mesoblast—in other words, from the mesoblast of the walls of the visceral clefts.

SECT. IV. *On the roots of the cranial nerves.*

The conception that each spinal segment gives origin to three roots, viz. anterior, posterior, and lateral, combined with the further conception that these three roots may be grouped together into a dual arrangement of somatic and splanchnic roots, each of which is composed of a ganglionated and a non-ganglionated portion, gives us a clue by which the homologies of the cranial nerves can be easily explained. The differentiation of these roots, which we have seen in its commencement in the cervical region, becomes more and more established as we pass beyond the limits of the 1st cervical segment to the segments above.

So long as the conception of a spinal nerve was confined to two roots, of which the one was anterior and motor while the other was posterior and sensory, the homologies of the cranial with the spinal nerves had to contend with two great difficulties. In the first place, how could such a nerve as the vagus be regarded as a posterior root when it possessed motor fibres ? In the second place, how can we account for the ganglia which are found in connection with such motor nerves as the oculomotor and facial ? These difficulties immediately vanish as soon as we consider that each cranial segment, similarly to each spinal segment, must give origin not only to a somatic root—in other words to non-ganglionated motor nerve fibres in connection with an anterior group of cells and ganglionated sensory fibres in connection with a posterior group of cells—but also to a splanchnic root, i. e. to large non-ganglionated motor nerve fibres in connection with a lateral group of cells and small

ganglionated fibres in connection with cells corresponding to Clarke's column.

Up to this point I have entirely ignored the existence of an important group of nerve fibres, without which each nerve segment is incomplete; these nerves are the nerves of ordinary sensation found in connection with the viscera. As long as I was dealing only with spinal nerves it was possible to pass them over in silence with the intention of considering them thoroughly when I came to speak of the afferent nerves of the visceral system; it is however impossible to trace the homologies between the cranial and spinal nerves without taking into account all the factors which make up a segmental spinal nerve group; for the characteristic of the cranial nerves is the more complete separation of these several factors into separate nerves with separate centres of origin.

The plan of the origin of the nerves of each spinal segment which I have put forward and the nomenclature which I have used in describing this plan, is based to a large extent upon the division of the motor nerves of skeletal muscles into two groups, one of which has close relations with the ramus visceralis. This hypothesis is united with the further suggestion that the large motor area of the anterior horn is naturally divided into two centres of origin for the nerve supply of these two muscular groups. Taken together, these two centres of origin (the anterior and lateral cell columns) form a single group characterized by the same large multipolar cells and give origin to similar large medullated motor nerves. We may, in fact, in the first instance describe a single anterior column of large multipolar cells as the centre of origin to the large medullated nerve fibres which form the motor nerves of all skeletal muscles. A closer analysis shows that this cell column is divisible into two, viz. an anterior and a lateral column, which, according to the hypothesis put forward here, give origin to the somatic and splanchnic skeletal muscles respectively. All experience teaches us that it is natural to group together voluntary motor nerves and ordinary sensory nerves. Apart from the nerves of special sense, we mean by the term "sensory" a nerve of ordinary sensation; such nerves are found in connection with two distinct surfaces, viz. the ectodermal and the endodermal surfaces. The first set terminates in the skin, the second set in the lining membranes of the different viscera. The nerves of ordinary sensation therefore, like the motor nerves of skeletal muscles, are divisible into a somatic and splanchnic group. Without discussing further the structure of

posterior roots it is evident that the ordinary sensory nerve is characterized by the large size of its medullated fibres. It is therefore reasonable to look upon the large medullated fibres which are found sparingly in the ramus visceralis and in the splanchnic nerves as the splanchnic sensory nerves; these fibres, as already mentioned, pass over the ganglia of the lateral and collateral chain and never communicate with their nerve cells. At present I see no chance of tracing these fibres separately to their origin in the spinal cord; there is certainly no good reason for connecting them especially with Clarke's column of cells. If, as I believe, they are sensory in function, they in all probability arise in close connection with the similarly constructed cutaneous sensory nerves, i. e. in the nerve cells of the posterior horn. These nerve cells form a distinct group different in character from those of the anterior horn and from those of Clarke's column: a sensory group which can be recognized by their appearance wherever found, just as much as the motor nerve cells of the anterior group. I imagine therefore that we must look upon this sensory cell column as double, one part belonging to the somatic and the other to the splanchnic sensory nerves, in precisely the same way as the motor cell column has been separated into an anterior somatic and a lateral splanchnic cell column.

Already we see indications of such a separation. Schwalbe speaks of two groups of nerve cells in the posterior horn, with both of which he imagines sensory nerve fibres to have connection, viz. the nerve cells found in connection with the substantia gelatinosa of Rolando, and those which he describes as the "solitary ganglion cells of the posterior horn[1]." This latter group of cells, as is seen in the figure referred to, is much more closely related to the cells of Clarke's column and to the lateral horn than to the substantia gelatinosa. In following up the homologies of the cranial nerves I propose then to take into account the possibility of the separation of the posterior horn into two parts, of which the one would be characterized by the presence of the substantia gelatinosa and the other would be the continuation of the "solitary ganglion cell column" of the posterior horn, and would therefore be recognisable by the structure of its ganglion cells.

Again, both sets of sensory fibres are doubtless connected with the posterior root ganglia, so that in considering the nature of the ganglia of the cranial nerves we must bear in mind the possibility that the

[1] Schwalbe, *Neurologie*, 1881, p. 347. Cf. Fig. 221.

posterior root ganglion may be divided into two portions, one of which is connected solely with splanchnic sensory and the other with somatic sensory nerves.

Disregarding for the moment the question of segmental arrangement, we can determine to which roots the different cranial nerves belong to some extent by their function, but chiefly by the position of the groups of nerve cells from which they arise.

Taking first those nerves which arise from cell groups which are clearly the continuation of the cell column of the anterior horn, i.e. nerves which represent the non-ganglionated somatic roots of the cranial segments, we find that the xiith, vith and iiird nerves clearly correspond both in their origin and in their function to such roots. The only other nerves which can by any possibility be included in this group are the ivth and part of the viith. The investigations of Van Wijhe seem to show that the ivth nerve belongs to the same category as the iiird and vith; it must therefore be classed among the non-ganglionated somatic roots. The position of the viith nerve appears clear; according to a large number of observers[1] the motor fibres of this nerve arise partly from the same group of nerve cells as the vith nerve; some of its fibres therefore arise from the continuation of the cell column of the anterior horn; and it is to my mind highly suggestive that the very muscles which remain unaffected in cases of bulbar paralysis are, according to Schwalbe[2], the *m. orbicularis oculi* and the *m. frontalis*; in these cases the nucleus of the vith nerve is always found to be unaffected by the disease, although the facial nucleus may be utterly destroyed. According to the views which I have suggested as to the difference of origin between the skeletal muscles supplied by splanchnic and somatic roots respectively, it is clear that the muscles supplied by the facial nerve can be divided into two groups: (1) Charles Bell's group of muscles connected with respiration, i.e. a splanchnic group, and (2) muscles unconnected with respiration but connected with the dermal covering, i.e. a somatic group. Clearly the m. orbicularis oculi and m. frontalis must be included in this latter group and not in the former.

The anterior or non-ganglionated somatic roots of the cranial nerves can be represented as follows:

[1] Cf. Schwalbe, *Op. cit.* p. 673.   [2] *Op. cit.*

Anterior motor or non-ganglionated somatic roots of cranial nerves.

Description of nerve	Muscle supply (Van Wijhe)
III (voluntary motor part)	Muscles derived from 1st somite
IV	do. do. 2nd ,,
VI	do. do. 3rd ,,
VII (that part which arises from same nucleus as VI)	
XII	do. 7th, 8th, 9th ,,

How far the 4th, 5th, and 6th somites take part in the formation of the muscles supplied by the anterior portion of VII can not be determined at present.

As far as these roots are concerned the guide to their segmental arrangement is to be found in the arrangement of the mesoblastic somites or myotomes.

All other voluntary muscles supplied by cranial nerves belong to the splanchnic voluntary muscular group, and are supplied by motor nerves which arise from the continuation of the cell column of the lateral horn. Thus we find in the first instance the motor fibres of the XIth nerve arising from this tract, above their origin we find the nucleus ambiguus giving origin to the motor voluntary nerves belonging to the vagus and glossopharyngeal, then next comes the lateral nucleus of the facial giving origin to the majority of the facial muscles, and finally as the continuation of the same lateral cell column the origin of the motor portion of the trigeminal[1].

The non-ganglionated lateral or splanchnic roots of the cranial nerves can be represented as follows:

[1] Hill. "Plan of Central Nervous System." Cambridge, 1885.

Lateral motor or non-ganglionated splanchnic roots of cranial nerves.

Description of nerve	Muscle supply (Van Wijhe)
v (motor portion)	Muscles derived from the lateral plates, i. e. from the mesoblast of the walls of the various visceral and gill clefts of the head
VII (that part which arises from the lateral nucleus)	
IX, X (that part which arises from the nucleus ambiguus)	
XI (that part which arises from the lateral horn)	

The guide to the segmental arrangements of these nerve roots is to be found in the arrangement of the visceral and branchial clefts.

Next in order we come to the rest of the lateral roots of the cranial nerves, viz. the ganglionated splanchnic roots: roots which are in special relation to the nerve cells of Clarke's column.

We have seen that this portion of the lateral root with its characteristic fine medullated nerve fibres formed the chief portion of the medullary roots of the spinal accessory; these roots continue without interruption into the formation of both vagus and glossopharyngeal nerves; a large portion of these nerves with their respective ganglia, the ganglion trunci vagi and the ganglion petrosum glosso-pharyngei is undoubtedly the continuation within the cranium of this ganglionated splanchnic portion of a spinal nerve segment. Above the glossopharyngeal we find belonging to the same group the n. intermedius with its ganglion geniculatum, and still higher the lateral root of the oculomotor with its portion of the ganglion ciliare.

We must also place the ganglionated root of the hypoglossal in this group. This fine rootlet with its ganglion arises in the dog among the rootlets of the medullary portion of the accessory nerve, and passes across to join the hypoglossal. In Pl. I., Fig. 5 I give an accurate representation of a section of this root after it has joined the main hypoglossal stem; the close resemblance between its structure and that of the fine-fibre portion of the spinal accessory (Pl. I., Fig. 1) point clearly to its connection with the lateral ganglionated root rather than with posterior roots.

Again, the origin of these nerves confirms the view arrived at from their distribution outside the skull. In the first place the portion of the nucleus of the vagus and glossopharyngeal nerves which lies between the posterior part of the vagus nucleus and the hypoglossal nucleus is not only in the proper position for the continuation of Clarke's column, but also is composed of the same kind of nerve cells as that column: cells therefore which are different to those which are found in the posterior part of the vagus nucleus, these latter resembling the sensory nerve cells of the posterior horn. The upper portion of this continuation of Clarke's column is according to Duval in connection with the n. intermedius. The origin of the lateral root of the oculomotorius is at present entirely unknown.

The lateral ganglionated or ganglionated splanchnic roots of the cranial nerves can be represented as follows:

Lateral ganglionated or ganglionated splanchnic roots of the cranial nerves.

Description of nerve	Ganglion of nerve
III (lateral root)	gangl. ciliare
VII (n. intermedius)	gangl. geniculatum
IX	gangl. petrosum
X, XI	gangl. trunci vagi
XII	gangl. hypoglossi

The guide to the segmental arrangement of these roots is to be found in the arrangement of the visceral and branchial clefts.

Finally we reach the consideration of the posterior roots of the cranial nerves.

If the two first cranial nerves are to be included in the same category as the rest, then they certainly must be included among the posterior roots; apart however from them we find distinct posterior roots, in the sensory root of the vth, in the vIIIth, and in the IXth and Xth nerves. In all these cases the characteristics of the posterior root

are present; viz. the presence of sensory fibres, the presence of a root ganglion, and the origin of the fibres from the continuation of the cell column of the posterior horn.

A closer examination shows that these posterior roots are not all of the same character; they are directly divisible into two groups; (1) those which are sensory to cutaneous surfaces such as the sensory portion of the trigeminal, the auditory, the optic and olfactory nerves; and (2) those which are sensory to internal surfaces such as the sensory nerves of the vagus and glossopharyngeal.

We see also that in the medulla oblongata the posterior horn is split into two parts; one part forms the posterior portion of the vagus and glossopharyngeus nucleus; and the other, which carries off with it the whole of the substantia gelatinosa of Rolando, lies always in close apposition with the ascending root of the vth nerve.

Throughout we find that the ascending root of the vth and the sensory nucleus of the vth is in close relation to the substantia gelatinosa; so too the origin of the auditory nerve is connected closely with the substantia gelatinosa. In other words, all those nerves which are somatic sensory nerves arise from that part of the sensory cell column which is in close connection with the substantia gelatinosa. On the other hand the posterior nucleus of the vagus and glossopharyngeal nerves with its characteristic sensory nerve cells is in close connection with the continuation of Clarke's column, and may fairly be looked upon as an enlargement of the cell group, previously spoken of, which Schwalbe defines as the group of solitary ganglion cells of the posterior horn. In other words, all those nerves which are splanchnic sensory nerves arise from that part of the sensory cell column which is in the neighbourhood of Clarke's column.

If subsequent investigation should confirm this conclusion, then this group of sensory ganglion cells might receive the name of the splanchnic sensory column, instead of as at present the group of solitary cells of the posterior horn.

Doubtless the investigation of the origin of the posterior roots of the vagus group in the Fishes, where undoubtedly both somatic and splanchnic sensory fibres exist, will throw light not only upon the difference in the origin of these two sets of fibres but also will help to explain the difference of position of the ascending roots of the trigeminal and vagus; both these bundles of nerve fibres are sensory in function, yet the former in its course from the spinal cord to its exit in the hind-brain lies always in close contiguity to the substantia gelatinosa of Rolando, while the latter

remains throughout in close relationship to the lateral or splanchnic area of grey matter.

The posterior roots of the cranial nerves can be represented as follows:

Posterior sensory roots of cranial nerves.

Description of nerve	Ganglion of nerve
I	
II (?)	
V (sensory portion with ascending root)	gangl. Gasseri part of gangl. ciliare (?)
VIII	ganglion of root
IX	gangl. jugulare
X (with ascending root)	gangl. jugulare

The guide to the segmental arrangement of the somatic sensory portions of these roots is probably to be found in the arrangement of the segmental sense organs (Beard and Froriep). On the other hand, the splanchnic sensory portions must be arranged in accordance with the visceral and branchial clefts.

We see then that the cranial nerves taken as a whole are founded on the same plan as the spinal nerves, the key-note of the arrangement in each case being firstly a triple arrangement of the nerve roots into anterior, lateral and posterior roots, and secondly the rearrangement of these three roots into a dual arrangement of splanchnic and somatic roots. It is to my mind perfectly clear that no correspondence exists between each of the so-called cranial nerves and such a perfect spinal nerve as is met with in the thoracic region; in order to obtain a cranial segment comparable to any one of the thoracic segments, parts of different cranial nerves must be pieced together; just as in the cervical region the 1st cervical nerve segment, for instance, is not complete without taking into account that part of the spinal accessory and of the ascending roots of the trigeminal and vagus which belong to that segment.

The arrangement of the cranial nerves into a number of separate segments in accordance with their phylogenetic development is the task of a morphologist rather than of a physiologist; I consider myself therefore very fortunate in having secured the aid of Dr Hans Gadow in this part of my research; in a separate paper to this one, I propose conjointly with him to point out the bearings of the conclusions arrived at in this paper upon the question of the segmental arrangement of the cranial nerves. For the present I propose to illustrate the formation of a cranial segment by the description of the three segmental nerve groups which arise from the mid-brain, hind-brain, and medulla oblongata, leaving for subsequent consideration the splitting up of these three main groups into their morphological segments.

An examination of the relative positions of the roots of the nerve group immediately above the 1st cervical nerve (see Fig. 8, Pl. IV.) demonstrates the presence of two sets of rootlets which correspond in position to the anterior and posterior rootlets of the 1st cervical nerve, the only difference being that they are not so directly opposite to each other: a slight shifting of position which is easily accounted for by the alteration in the direction of the spinal axis due to the opening out of the central canal, and the formation of the 4th ventricle.

The group of anterior rootlets stands alone and distinct; the group of posterior rootlets is however not so distinct, owing to the large number of lateral roots which arise in close proximity to it. If we imagine these lateral roots removed we should have two groups of rootlets left exactly corresponding to and metameric with the anterior and posterior roots of the 1st cervical nerve group. These two groups form the hypoglossal and the posterior roots of the vago-glossopharyngeal nerve respectively. The lateral roots of this group arise between their corresponding anterior and posterior roots in precisely the same way as in the nerve groups below; an extra complication being introduced simply by the fact that the lateral roots of the lower nerve groups have joined together to form a single nerve, which passes out at this level instead of each lateral root passing out with its own anterior and posterior root.

We see then that the neural segment immediately above the 1st cervical is formed by anterior, lateral, and posterior roots in the same way as the 1st cervical segment itself. We have seen also that the origin of these roots is the same as in the segments below, and that the ganglia on their roots are strictly homologous to the ganglia of other spinal segments. We can therefore say confidently the segment

above the 1st cervical is composed by the hypoglossal, accessory, vagus, and glossopharyngeal nerves; the hypoglossal forming its anterior root, the accessory, vagus, and glossopharyngeal its lateral and posterior roots.

The large size and importance of this segment, or as it might be called segmental nerve group, depend doubtless partly on its position and partly on the concentration of the original separate metameres which has taken place in the upper portion of the spinal axis; such concentration however is not confined to the cranial nerve groups; it is equally evident, though perhaps to a less extent, in all the cervical nerve groups. Here, as well as in the segments above, originally separate metameres have fused together to form one segment, and so the cervical nerve groups have been formed in precisely the same way as the large group formed by the hypoglossal, vagus, accessory and glossopharyngeal.

This latter large group may be described as the nerve group of the medulla oblongata, and its nerves supply the somites, gill clefts, and sense organs corresponding to the segments into which this group is divisible.

Above the medulla oblongata we find the group of nerves which proceeds from the hind-brain; the anterior roots of this nerve group are formed by the vith and part of the viith nerve; the lateral roots by the main portion of the viith, part of the motor portion of the vth nerve, and the n. intermedius (possibly also a part of the ixth nerve belongs to the hind-brain); the posterior roots are formed by the viiith and part of the sensory portion of the vth nerve.

These nerves taken together form the nerve group of the hind-brain and supply the somites, visceral clefts, and sense organs of the segments into which this group is divisible.

The uppermost group is formed by the nerves which arise from the mid-brain. In this group with the rudimentary character of the visceral clefts we find a corresponding rudimentary character of the lateral or splanchnic root.

The anterior roots of this region are formed by the iiird and ivth nerves; the lateral roots by a portion of the motor part of the vth nerve (descending root) together with possibly the lateral root of the iiird nerve; the posterior roots by the sensory portion of the descending root of the vth nerve in connection with the ganglion ciliare (?) and by the ist and iind (?) nerves with their specialized sense organs.

These nerves taken together form the nerve group of the mid-brain

and supply the somites, visceral clefts, and sense organs of the segments into which this group is divisible.

This division of the cranial nerves may be represented in a tabular form as follows:

	Roots of the cranial nerves.				
	Anterior	Lateral		Posterior	
	non-gangl. somatic	non-gangl. splanchnic	gangl. splanchnic	sensory splanchnic	sensory somatic
Mid-brain	III IV	V motor (descending root)	III (gangl. ciliare)		I II V sensory (descending root gang. ciliare ?)
Hind-brain	VI VII (part which arises from nucleus of VI)	V motor VII	VIII (n. intermedius with gang. geniculat.)		V sensory (gang. Gasseri) VIII
Med. oblongata	XII	IX X XI part which arises from lateral horn	IX (gang. petrosum) X XI (gang. trunci vagi) XII (gang. hypoglossi)	IX X ganglion jugulare with ascending root of X	V sensory (ascending root)
Centres of origin	Anterior column	Lateral column	Clarke's column	Sensory splanchnic column of post. horn	Sensory somatic column of post. horn

DESCRIPTION OF FIGURES.

PLATES I.—IV.

All the figures in Pl. I. and Pl. II., with the exception of Fig. 10, were drawn to the same scale under the microscope by means of the camera lucida. The exact size of each nerve fibre can be estimated by comparison with the scale in Pl. II.

All the figures in Pl. I. and Figs. 6, 7 in Pl. II. were made from preparations taken from the same large collie dog. Figs. 8, 9 were taken from another dog slightly larger than the collie.

PLATE I.

Fig. 1. Section of one of the upper rootlets of the spinal accessory nerve. The medullated fibres are imbedded in a connective tissue matrix, coloured of a yellowish tinge in the figure.

Fig. 2. Section of the large fibred part of the spinal accessory nerve. A portion only of the section is drawn in the figure.

Fig. 3. Part of a section through the anterior root of the 1st cervical nerve.

Fig. 4. Section of a rootlet of the hypoglossal nerve.

Fig. 5. Section of the ganglionated root (A) of the hypoglossal nerve after it has reached the main hypoglossal root (B). The connective tissue matrix is tinged yellow.

PLATE II.

Fig. 6.   Section of three anterior rootlets of the 9th spinal (1st thoracic) nerve.

Fig. 7.   Section of three anterior rootlets of the 10th spinal (2nd thoracic) nerve.

Fig. 8.   Section of the white ramus communicans (A) of the 11th spinal (3rd thoracic) nerve.   Near it is a section of a small grey ramus communicans (B) belonging to the same spinal nerve.   The non-medullated fibres as well as the connective tissue are tinged of a yellowish colour.

Fig. 9.   Part of a section through the ramus communicans of the 26th spinal (3rd lumbar) nerve.   This figure represents a typical grey ramus communicans.   The non-medullated fibres of which it is chiefly composed are tinged yellow in the figure.

Fig. 10.   Medullary roots of the vagus and accessory nerves as imbedded, in order to trace the accessory fibres through a series of sections up to the ganglion trunci vagi.   The sections were cut parallel to line *l*.

Ac.   Accessory nerve.

M.   Piece of medulla oblong. imbedded with the nerve roots.

J.   Position of ganglion jugulare vagi.

T.   Position of ganglion trunci vagi.

PLATE III.

The diagrams in this plate are constructed from dissections of the visceral nerves in the dog, with the exception of the cranial visceral nerves.   The arrangement of these latter was taken from Henle.   In all the figures those nerves which contain bundles of fine medullated fibres are coloured red; those which consist chiefly of non-medullated fibres are coloured blue.

Fig. 1.   Diagram to show the formation of the rami viscerales in the cervico-cranial, thoracic, and sacral regions, together with the general distribution of the visceral nerves.

Fig. 2.   Diagram to show the origin and distribution of the vaso-motor nerves.

Fig. 3. Diagram to show the origin and distribution of the inhibitory nerves of the circular muscles of the viscera, together with the inhibitory nerves of the sphincter muscle of the iris.

Fig. 4. Diagram to show the distribution of the motor nerves of the circular muscles of the viscera.

Fig. 5. Diagram to show the distribution of the vaso-inhibitory nerves.

PLATE IV.

I am indebted to the kindness of Mr G. Turner for the figures of this plate. Figures 2, 3, 4, 5 were drawn from photographs taken by him of the microscopic sections.

Fig. 1 shows the connection between the posterior root ganglia and the sympathetic chain in the tortoise. *Sy*, sympathetic chain; the numbers 2—7 are placed against the corresponding thoracic nerves. The line *l* shows the direction of the series of parallel sections taken through the roots, ramus communicans, and root ganglion of the 5th thoracic nerve.

Figs. 2, 3, 4, 5 are copies of 4 sections out of this series and show the formation of ganglion cells on the sympathetic nerves, *a*, *b*, *c*, and the ultimate amalgamation of these ganglion cells with those of the root ganglion.

Fig. 6. Section of that branch of the 2nd thoracic nerve which forms the communicating branch to the 1st thoracic nerve and also helps to form the ramus visceralis of the ganglion stellatum. (From a photograph taken with lens $\frac{1}{3}$ in.)

V. Small fibred portion of nerve which becomes the internal branch or ramus visceralis in connection with the ganglion stellatum.

A. Large fibred portion which becomes the external branch or branch of communication with the brachial plexus.

Fig. 7. Section of spinal accessory close to the ganglion jugulare vagi. (From a photograph taken with lens 1 in.)

V. Small fibred portion which becomes the internal branch or ramus visceralis in connection with the ganglion trunci vagi.

A. Large fibred portion which becomes the external branch and communicates with the cervical plexus.

Fig. 8.   Upper part of spinal cord of dog cut in two in order to show the arrangement of the upper cervical nerve roots and those of the neural segment immediately above them.

1, 2, 3.   Anterior and posterior roots of the corresponding cervical nerves.

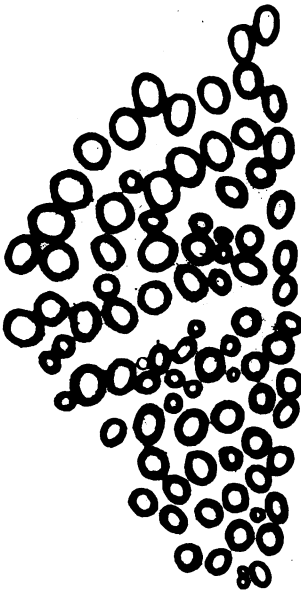*V.*   Vagus nerve.

H.   Hypoglossal nerve.

Ac.   Spinal accessory nerve.
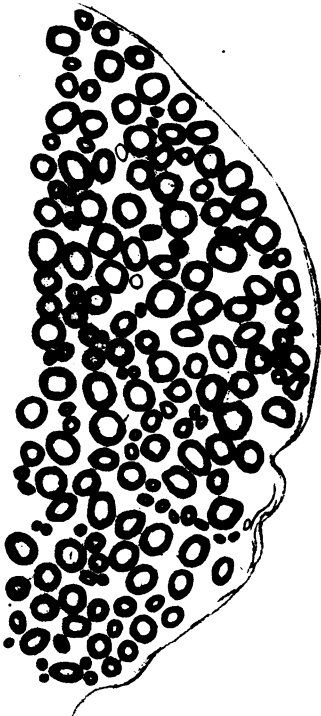
CAMBRIDGE,
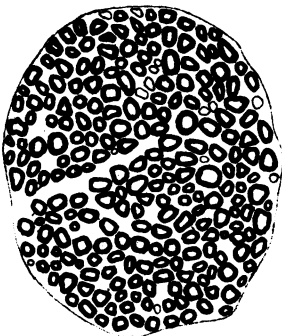*Dec.* 21, 1885.
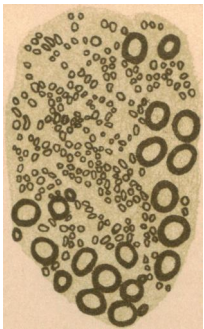
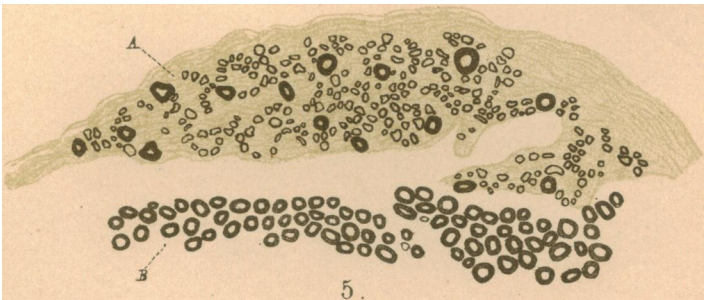THE BARTLETT
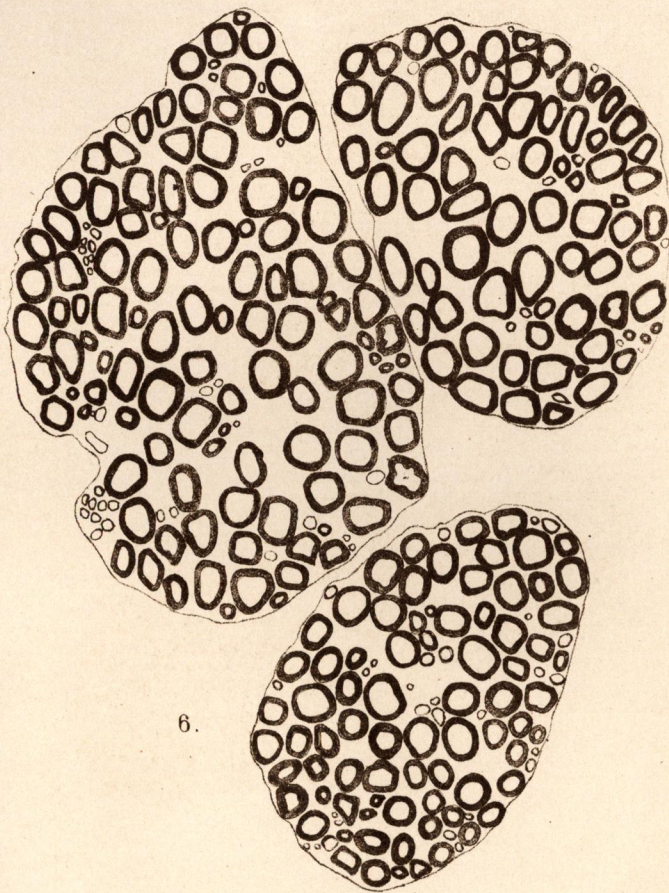CLINICAL CLUB,
MILWAUKEE, WIS.

1.

2.

3.

4.

5.

10 ⅒ Millimeter.   100 ⅒ Millimeter.

Zeiss Ocular lens D.

6.

7.

9.

8.

10.

Ac *T* *J* *V* *M* *A* *B*

Fig. I.

Fig. II.
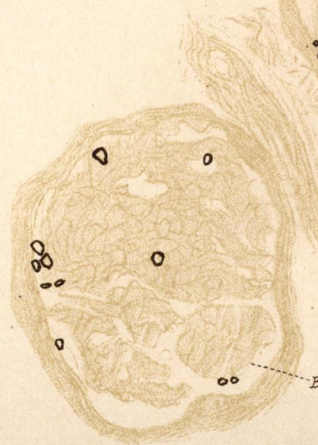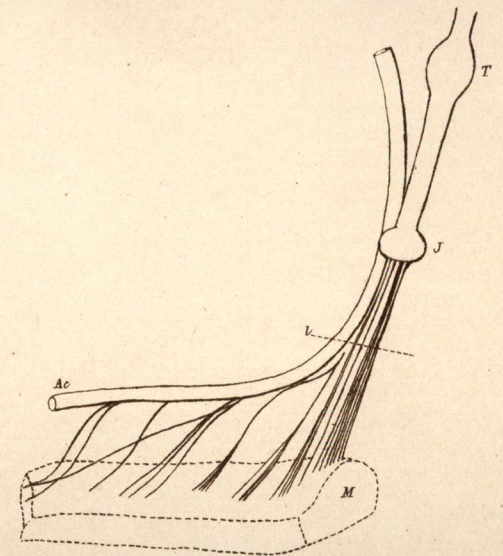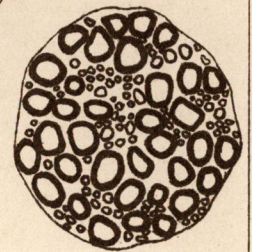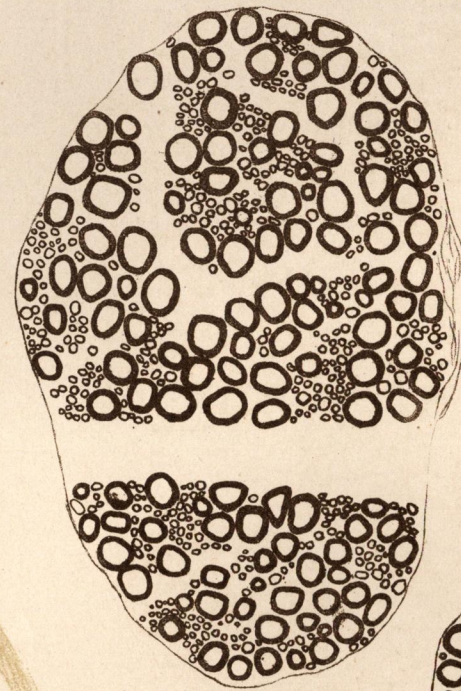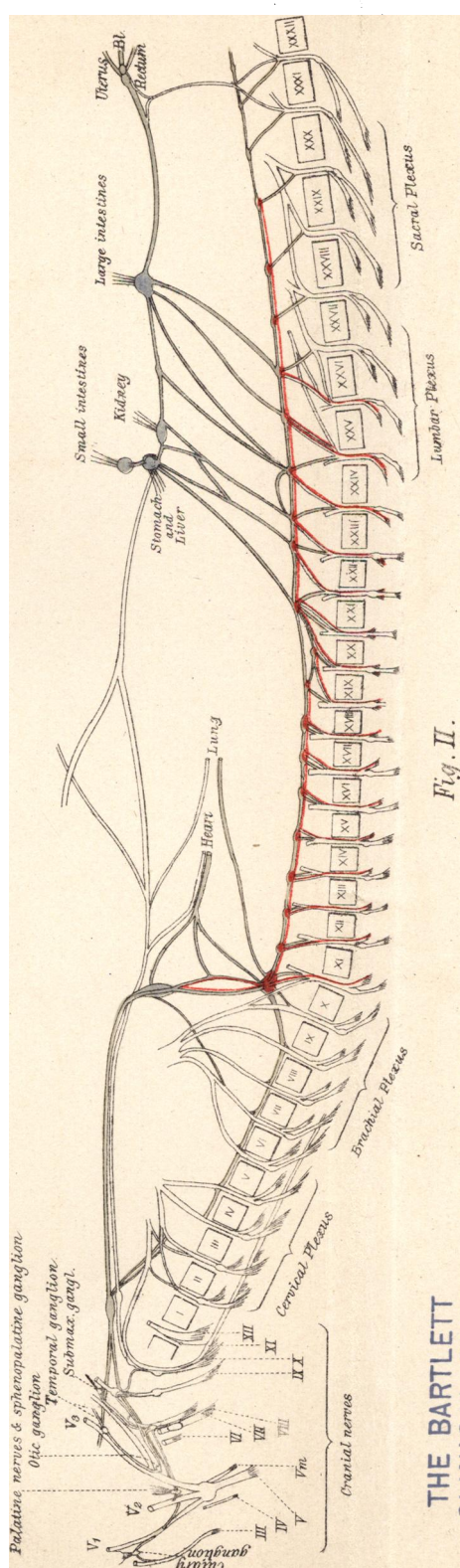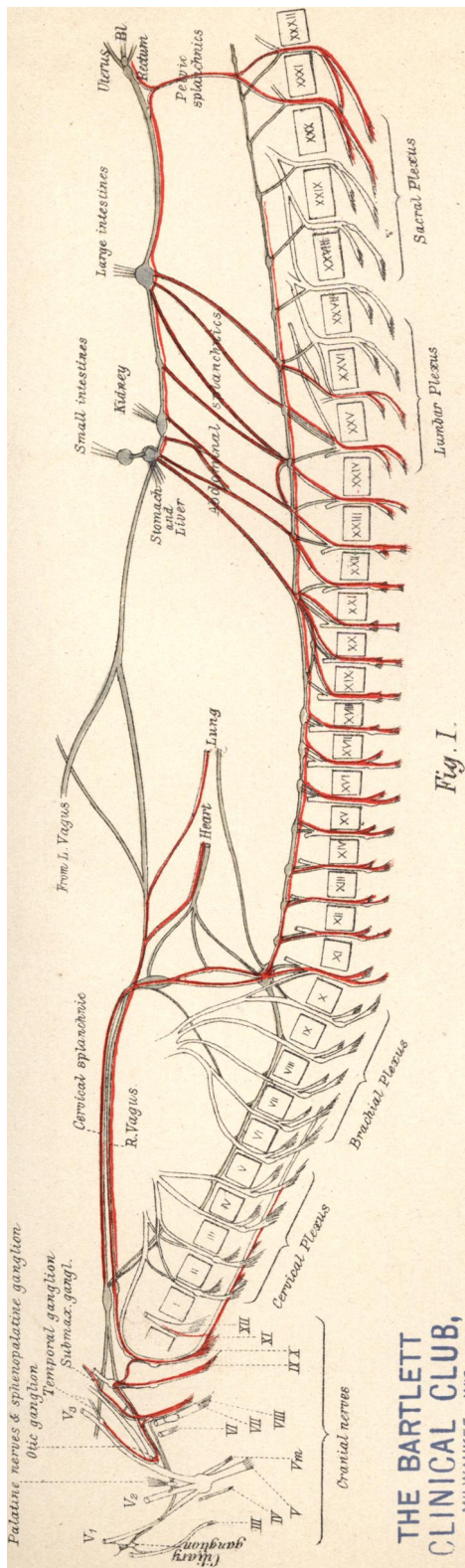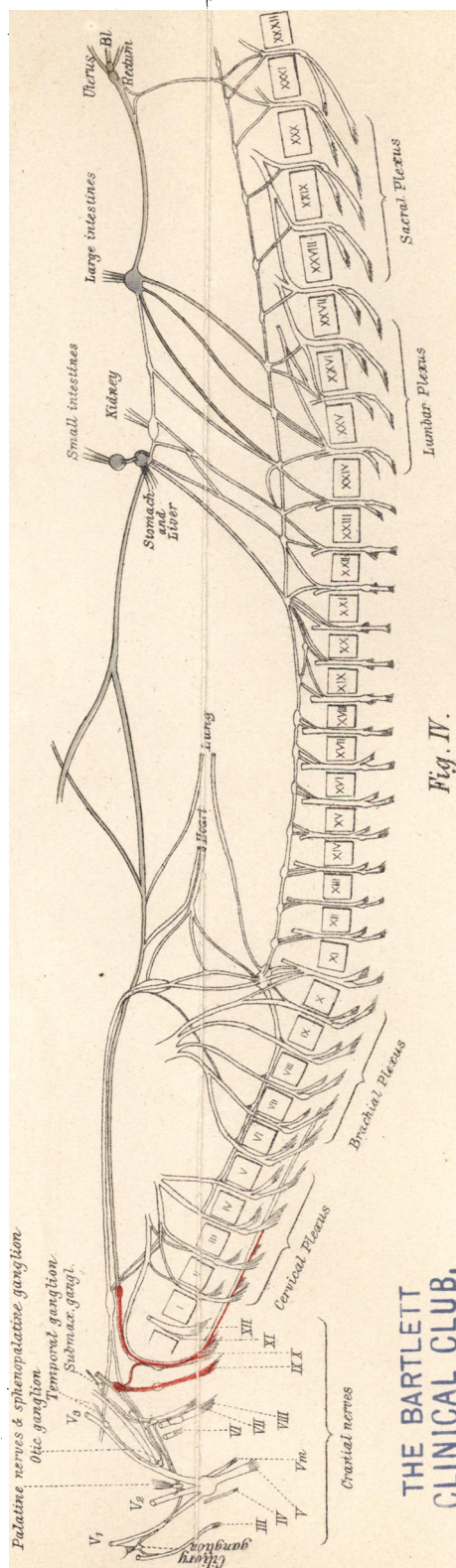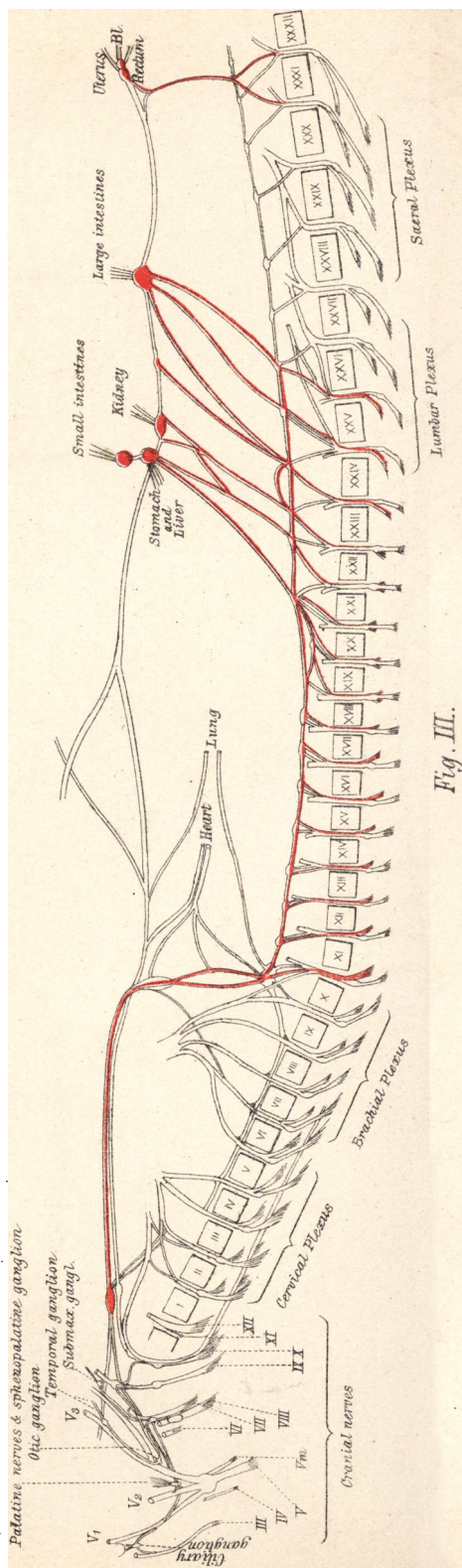
THE BARTLETT
CLINICAL CLUB,
MILWAUKEE, WIS.

THE BARTLETT
CLINICAL CLUB,
MILWAUKEE, WIS.

Fig. III.

Fig. IV.

Fig - V.

PLATE IV.

1.

2.

3.

4.

5.

6.

7.

8.